ISSN 00 22-09 81
JEMBAM 44 (2,3) 111–300 (1980)
, Volume 44, Number 2,3, pp. 111–300
Published 22 April 1980

JOURNAL

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XPERIMENTAL MARINE BIOLOGY

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JOURNAL OF EXPERIMENTAL MARINE BIOLOGY AND ECOLOGY

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Subscription information
The subscription price of a volume is Dfl. 132.– or U.S. $ 67.75, including postage.

Subscriptions should be sent to the publishers, **Elsevier/North-Holland Biomedical Press, Journal Division, P.O. Box 211, 1000 AE Amsterdam, The Netherlands.**

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Library of Congress Catalog Card Number 68–26535

Printed in Belgium

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J. exp. mar. Biol. Ecol., 1980, Vol. 44, pp. 111–132
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MOVEMENT, MORPHOLOGY, REPRODUCTIVE PERIODICITY, AND SOME FACTORS AFFECTING GONAD PRODUCTION IN THE SEASTAR *ASTROSTOLE SCABRA* (Hutton)

JOHN C. TOWN

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Abstract: At Kaikoura, New Zealand (42°25′S : 173°42′E), tagged, immature *Astrostole scabra* (Hutton) usually remained within intertidal pools for <30 days. There was no seasonal vertical migration or intermixing of sub-populations. Intertidal seastars were smaller, had a thicker skeleton, and were damaged more frequently than their subtidal counterparts.

The onset of sexual maturity in this species occurred coincidentally with the adoption of an exclusively subtidal habitat (20–146 m), the attainment of a radius of at least 110 mm, and a reduction in skeleton thickness. In 1975, 1976, and 1977, spawning was in late August–early September. Gametogenesis commenced in February–March. There was no seasonal inverse correlation between gonad and pyloric caeca indices.

In undamaged, subtidal seastars of both sexes, gonad production was related to body size such that the volume of gonad produced by August increased linearly with respect to eviscerated wet weight. Regeneration partly suppressed gonad production, and large intertidal seastars had reduced gonad indices. The periodicity of reproductive events could not be correlated unequivocally with any physical or biotic exogenous environmental factor.

INTRODUCTION

The aims of this study were to determine, by tagging of individual starfish, the emigration and immigration rates, and residence periods of *Astrostole scabra* (Hutton) in selected intertidal pools. The radius, eviscerated wet weight, and gonad index of both intertidal and subtidal seastars were measured to see whether any differences existed in their size, morphology and reproductive potential. The annual reproductive cycle was outlined by organ index methods to discover if any seasonal relationship existed between the size of gonads and pyloric caeca.

Asteroids undertake typically restricted movement of no more than about 10 m/day (Dayton *et al.*, 1974; Pabst & Vincentini, 1978). *Astropecten* species have daily activity patterns (Mori & Matutani, 1952; Massé, 1975; Ferlin-Lubini & Ribi, 1978). Burla *et al.* (1972) noted site faithfulness in small *A. aranciacus* and Wilson & Marsh (1974) suspected the existence of a "home base" for *Acanthaster planci* in Western Australian waters. Paine (1976) found little intermixing of sub-populations of *Pisaster ochraceus*, and noted that individuals would remain within an area bounded by only poorly defined barriers. These findings complemented those of Landen-

berger (1966) who reported that *P. giganteus* stayed within an area likely to yield food.

Sexual maturity in some seastar species depends on size (Mead, 1900) whereas in others, gonad production is independent of size or age (Vevers, 1949). Many authors have suggested that reproductive potential in seastars is linked directly to the abundance and type of available food (Pearse, 1965; Birkeland, 1974), and Crump (1971) proved this dependence experimentally in *Patiriella regularis*. The inverse relationship between the size of gonads and pyloric caeca in *Pisaster ochraceus* and *P. brevispinus*, is related to seasonal feeding patterns as food reserves are stored in the pyloric caeca before transfer to the developing gonads (Farmanfarmaian *et al.*, 1958; Mauzey, 1966). The predominant reproductive mode in asteroids is the free liberation of gametes and these typically small eggs develop into planktotrophic larvae (Feder & Christensen, 1966). Most starfish have a fairly restricted spawning season (Boolootian, 1966), although three asterinids, *Patiria miniata*, *Patiriella vivipara*, and *P. exigua* have the potential to breed throughout the year (Lawson-Kerr & Anderson, 1978).

Apart from Crump's (1971) account of reproductive periodicity in *Patiriella regularis*, little substantial information has been published on the reproductive habits of New Zealand seastars. Bennett (1927) reported autotomous reproduction in *Allostichaster insignis*, *A. polyplax*, and *Coscinasterias calamaria*, and Emson (1978) described the process of fission in *Allostichaster polyplax*. Fell (1959) noted the brooding habit of *Calvasterias suteri*. Little is known about the reproductive biology of *Astrostole scabra*. Maxwell (1957) obtained fertilizable gametes from specimens in the Wellington region in October 1954, and raised the larvae through to the pelagic bipinnaria stage. *A. scabra*, a forcipulate asteriid, is New Zealand's largest seastar (Fell, 1959), can grow to a radius of 365 mm, and is widely distributed in New Zealand waters at depths of 0–146 m (Town, 1979b).

Materials and Methods

LOCATION

The study was conducted from the Edward Percival Marine Laboratory situated at Kaikoura (42°25′S : 173°42′E) on the eastern coast of New Zealand's South Island. The tides of the region are semidiurnal with a spring tide range of 1.6 m and a neap tide range of ≈0.8 m. The interaction of prevailing surface currents and a complex local submarine topography supply the Kaikoura region with cold temperate mixed water (Knox, 1960). Inshore waters have an annual temperature range of 8.5 °C–19.0 °C and surface salinities remain between 33.8‰ and 34.6‰ throughout the year (Bradford, 1972). The positions of the four intertidal stations used in the study are shown in Fig. 1. Site 1 is an extensive intertidal platform, consisting of

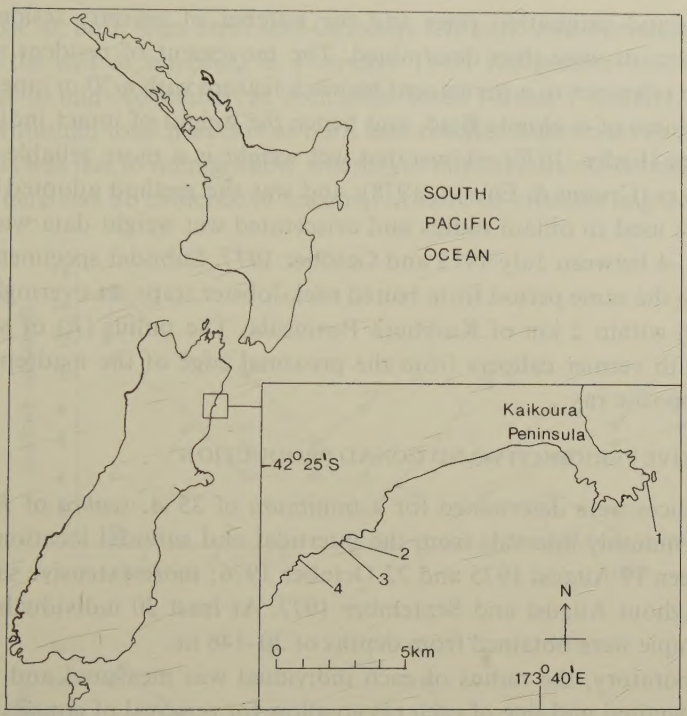

Fig. 1. Locations of four intertidal sampling stations.

Tertiary limestone, on the northern face of Kaikoura Peninsula. Sites 2, 3, and 4 are three of many bedrock shore platforms which form a narrow strip of coastline south of Kaikoura Peninsula.

MORPHOLOGY AND MOVEMENT

Between May 1977 and February 1978, individual *A. scabra* were tagged in the field with a solution of Nile Blue sulphate (1 g/l) which was taken up by the tube feet and adambulacral spines. Although this stain was retained for up to six months, it was re-inforced whenever seastars were recaptured. Individual rays were stained selectively and many combinations could be obtained by using the excentric madreporite as a reference point. Thus, individual starfish were recognizable. Two pools at Site 1 were selected for tagging experiments because they contained seastars throughout the year, had restricted access to the open sea, were subjected to minimal public disturbance, and rocks under which seastars occurred were large, individually identifiable, and immobile. The first pool (Site A), was 45 m long, 0.1–2.0 m wide, and no more than 1 m deep during low tide. The second pool (Site B) was 12.9 × 10.2 m and was also <1 m deep during low tide. Each pool was visited at least monthly and the number of stained and unstained animals noted. Immigrants were stained.

Immigration and emigration rates and the number of seastars resident between inspection periods were then determined. The movement of resident starfish was measured by reference to a permanent bedrock feature with a 30 m tape measure.

As the volume of coelomic fluid, and hence the weight of intact individual starfish may vary (Feder, 1970), eviscerated wet weight is a more reliable measure of size in seastars (Crump & Emson, 1978), and was the method adopted here. Intertidal seastars used to obtain radius and eviscerated wet weight data were collected from Sites 1–4 between July 1975 and October 1977. Subtidal specimens were collected during the same period from baited rock-lobster traps set overnight at depths of 20–146 m within 2 km of Kaikoura Peninsula. The radius (R) of seastars was measured with vernier calipers from the proximal edge of the madreporite to the tip of the opposite ray.

REPRODUCTIVE PERIODICITY AND GONAD PRODUCTION

Organ indices were determined for a minimum of 25 *A. scabra* of $R \geqslant 110$ mm collected at monthly intervals from the intertidal and subtidal locations described above between 19 August 1975 and 22 October 1976; more extensive samples were taken throughout August and September 1977. At least 20 individuals from each monthly sample were obtained from depths of 20–146 m.

In the laboratory, the radius of each individual was measured and a slit made along the abactinal mid-line of each ray to allow for removal of gonads and pyloric caeca. The eviscerated body was then drained, blotted, and weighed. The displacement volume of gonads and pyloric caeca, drained of surface moisture, was measured separately in a graduated measuring cylinder. Gonad and pyloric caeca indices were calculated according to Farmanfarmaian *et al.* (1958) and Pearse (1965). The ratio of organ volume to eviscerated wet weight $\times 100$ was taken as the organ index. The specific gravity of these organs did not differ significantly from that of water, so conversion to weight was unnecessary.

The sexes could not be distinguished externally. Internal examinations between March and August, however, revealed that ovaries were bright orange and testes creamy-white. Between September and February, smear preparations of dissected gonads were examined microscopically and the presence of oocytes or motile spermatozoa was noted. Spawning was considered to have occurred when a sharp drop in gonad indices was noted.

RESULTS

MOVEMENT

Numbers of seastars present at any time was similar, at Sites A and B with maxima of 15 (both sites) and minima of 5 and 8, respectively (Fig. 2). At Site A, emigration exceeded immigration from mid-June until late August so that total numbers fell. An identical situation was found at Site B until early August. Total

numbers rose at both sites until mid-October, fell until mid-November, and rose again until the end of sampling in February 1978. Emigration was highest from mid-October to mid-November, at both sites, when 10 and 9 seastars, respectively, departed. Although total numbers at both sites reached high levels in mid-October, at Site A this was due to immigration, whereas at Site B residents formed the bulk of the total. There was no evidence of seasonal inshore or offshore migration.

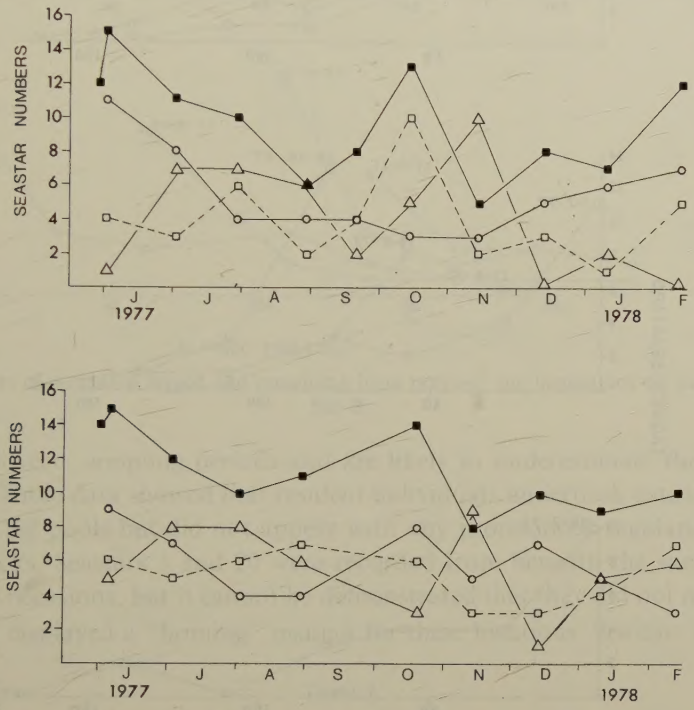

Fig. 2. Stained (○), immigrant (□), emigrant (△) and total (■) numbers of *A. scabra* at Sites A (upper) and B (lower) between June 1977 and February 1978.

Most seastars remained resident in the two pools for <30 days so the majority of tagged specimens left between site inspections (Figs 3, 4). Some individuals reappeared in subsequent searches. At Site A, seastars were never recovered more than 107 days after tagging, and only four specimens were recaptured more than four times. At Site B, three seastars were recovered 192 days after tagging but only four specimens were recaptured three or more times. The maximum number of recoveries of a single seastar in consecutive inspections was six at Site A and three at Site B. At neither location were any animals tagged in June 1977 still present in February 1978. There was no intermixing of individuals between the two sites, which were 100 m apart. The patterns of locomotion in seastars recaptured three or more times (Figs 5, 6) record only the net change in location of resident in-

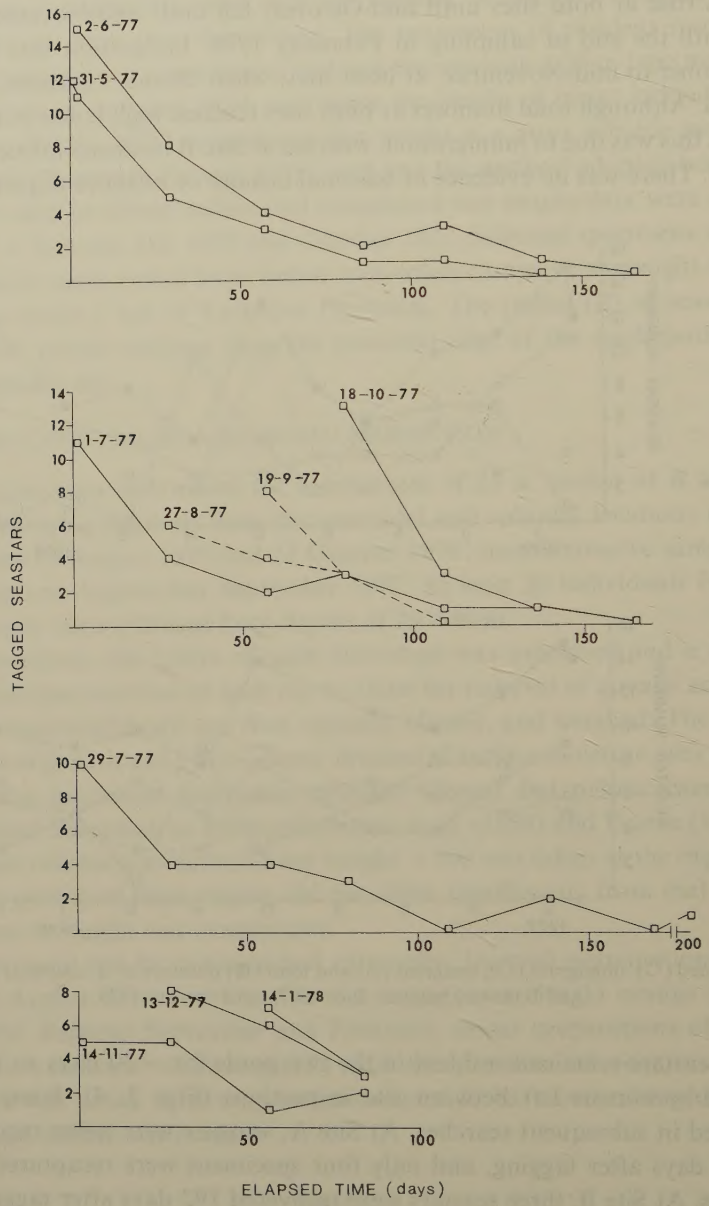

Fig. 3. Numbers of *A. scabra* tagged and remaining from previous site inspections on dates shown at Site A.

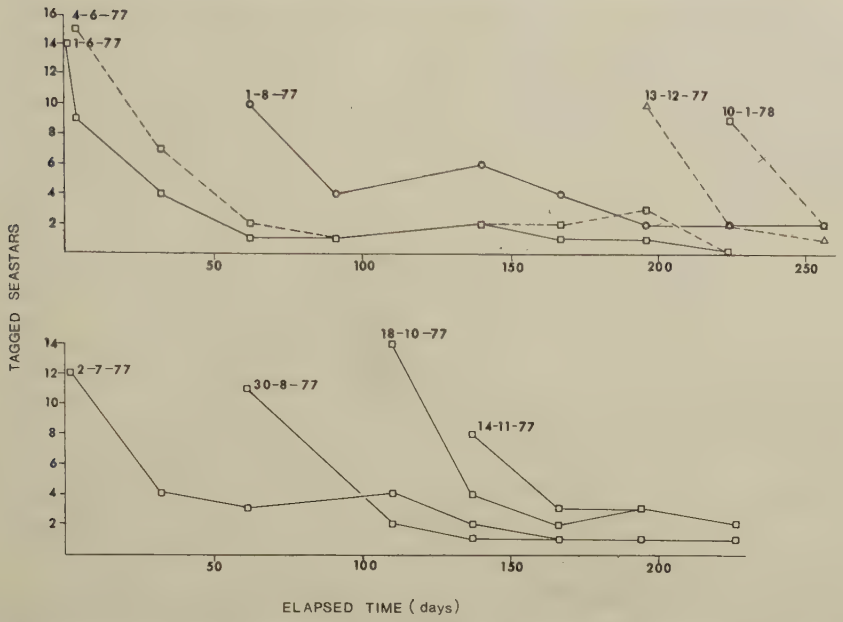

Fig. 4. Numbers of *A. scabra* tagged and remaining from previous site inspections on dates shown at Site B.

dividuals between sampling periods and are likely to underestimate the extent of movement. These data showed that resident individuals undertook extensive movement about the pools but did not appear with any pronounced regularity beneath the same rocks. Seastars 3 and 20 were recorded from beneath the same rock on two or more occasions, but it cannot be demonstrated that they did not move at all, or that they displayed a "homing" instinct for these locations. Seastars recaptured

TABLE I

Net distances (m) moved by resident *A. scabra* between site inspections.

Date	Time between site inspections (days)	Mean net distance moved					
		Site A			Site B		
		n	$\bar{x}$	SD	*n*	$\bar{x}$	SD
1 July 77	2	8	5.86	2.8	7	1.77	2.9
29 July 77	28	4	0.81	0.8	4	6.12	5.5
27 Aug. 77	28	4	0.21	0.1	4	4.42	2.0
19 Sept. 77	22	4	0.3	0.4	–	–	–
18 Oct. 77	28	3	0.8	1.3	8	4.34	3.8
14 Nov. 77	26	3	4.3	3.7	5	5.8	3.1
13 Dec. 77	28	5	4.2	2.2	7	4.6	2.6
10 Jan. 78	27	6	3.9	2.1	5	5.5	2.5
11 Feb. 78	31	7	3.4	1.3	3	3.8	1.8

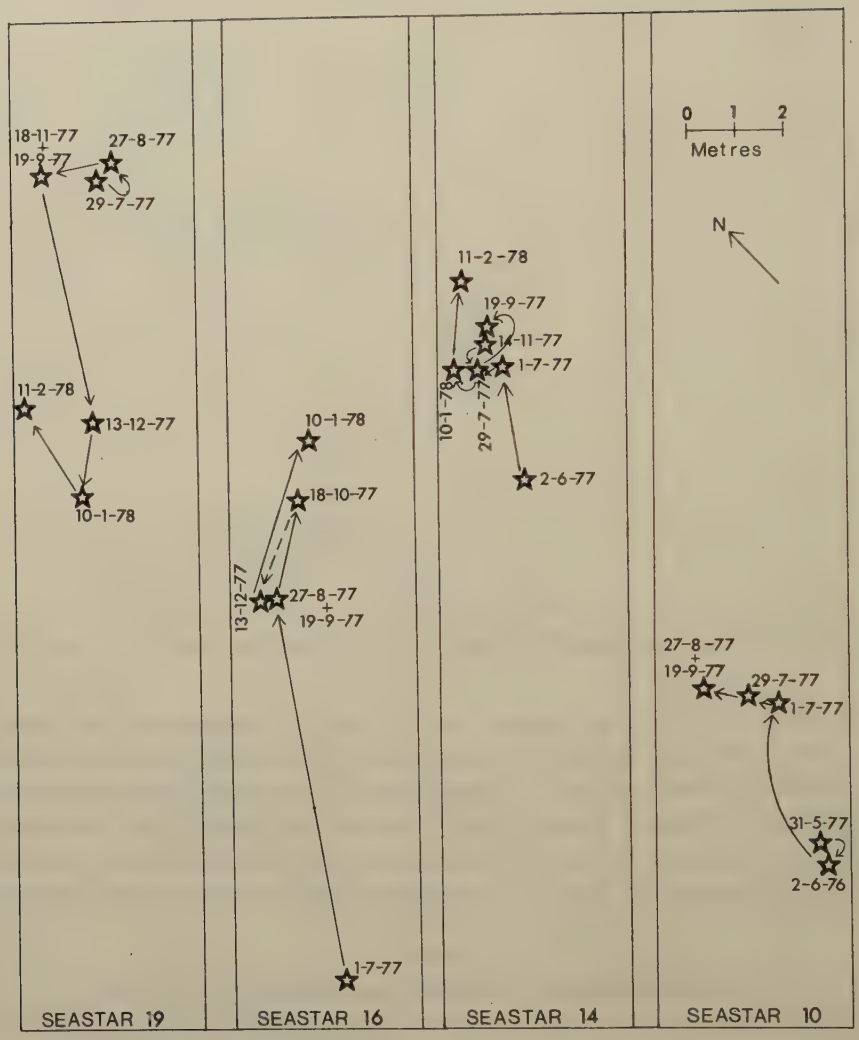

Fig. 5. Diagrammatic representations of patterns of locomotion of four *A. scabra* recaptured four or more times between consecutive (solid line) and non-consecutive (broken line) searches at Site A.

during non-consecutive searches probably emigrated from the pool only to return later. The largest net change in location recorded for a resident seastar in consecutive searches was 13.5 m (Seastar 25 between 2 July and 8 August 1977) (Fig. 6). Five types of movement could be recognized with respect to a pool; immigration, permanent emigration, temporary emigration, net movement within the pool, and no movement. Most specimens emigrated permanently. Except in early July, resident seastars at Site B moved consistently greater net distances than those at Site A (Table I). The long, narrow structure of the Site A pool meant that potential movements of seastars were more restricted than they were at Site B.

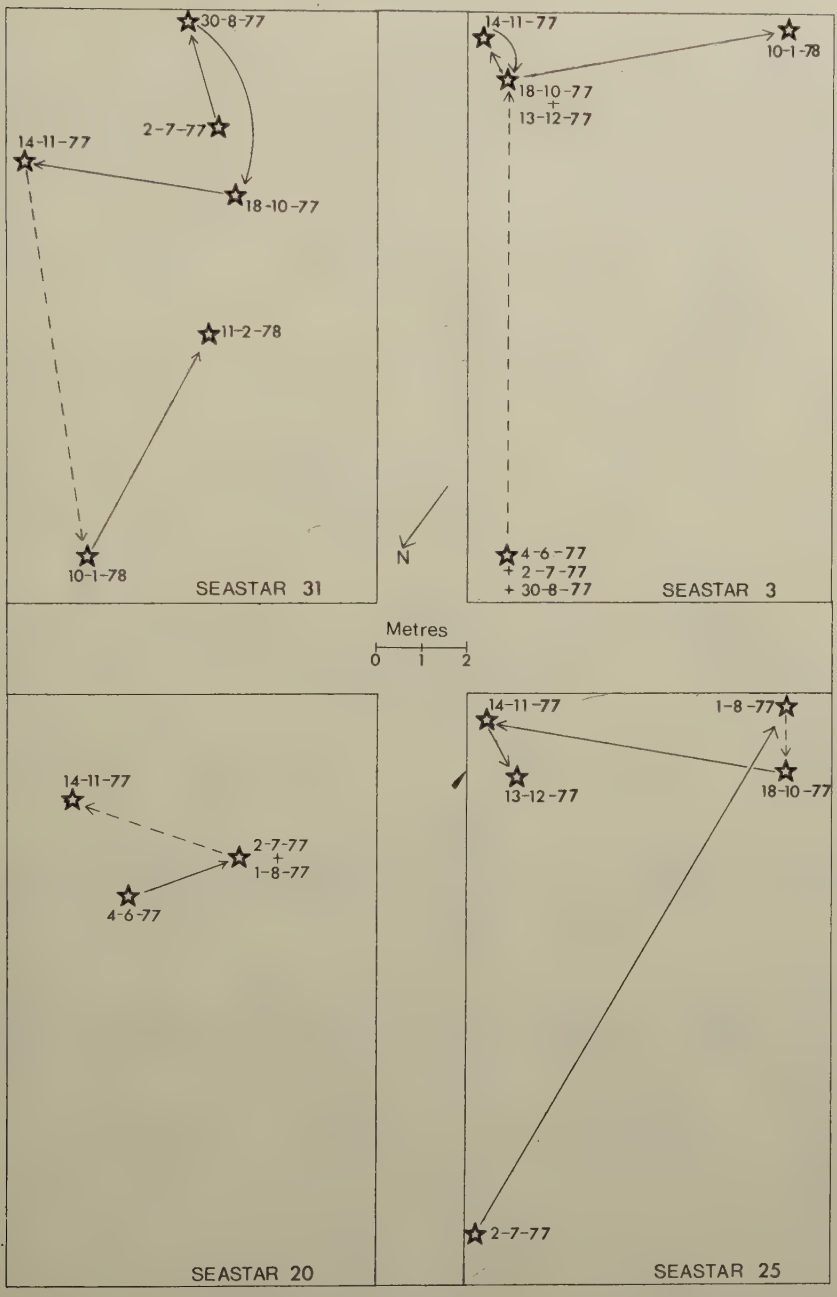

Fig. 6. Diagrammatic representations of patterns of locomotion of four *A. scabra* recaptured three or more times between consecutive (solid line) and non-consecutive (broken line) searches at Site B.

SIZE AND MORPHOLOGY

Size-frequency distributions of intertidal and subtidal *A. scabra* from Kaikoura differed markedly (Fig. 7). Few specimens of $R > 140$ mm appeared in intertidal collections (Fig. 8), whereas in all animals collected from depths of 20–146 m R was >110 mm. The mean radius of intertidal individuals did not change markedly during

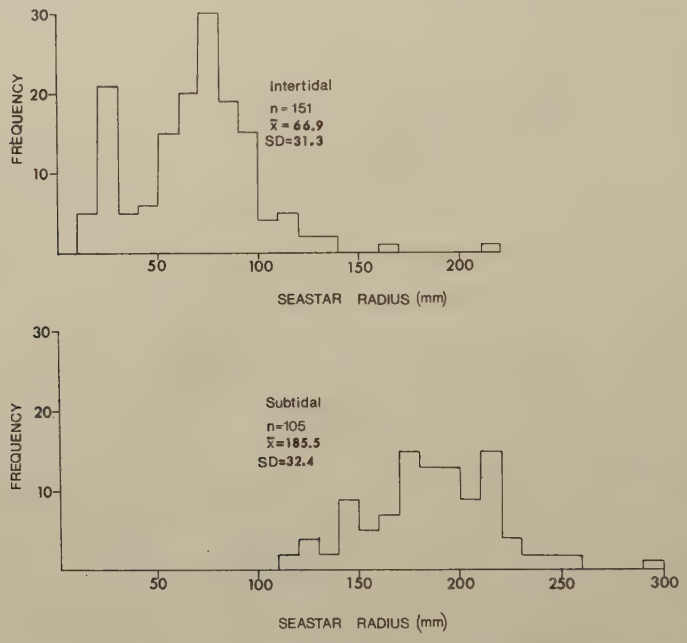

Fig. 7. Size frequencies of intertidal and subtidal (20–146 m depth) *A. scabra* measured in October 1976 when the largest sample of subtidal seastars was obtained.

TABLE II

Numbers of intertidal and subtidal *A. scabra* regenerating lost rays in October 1976: *n*, sample size.

No. of rays regenerating	Seastar numbers: Intertidal ($n = 151$)	Seastar numbers: 20–146 m ($n = 105$)
1	12	5
2	6	2
3	2	1
4	4	1
5	2	–
6	3	–
Total	29	9
% of sample	19.2	8.5
% of total regenerating 1 ray	41.3	55.5

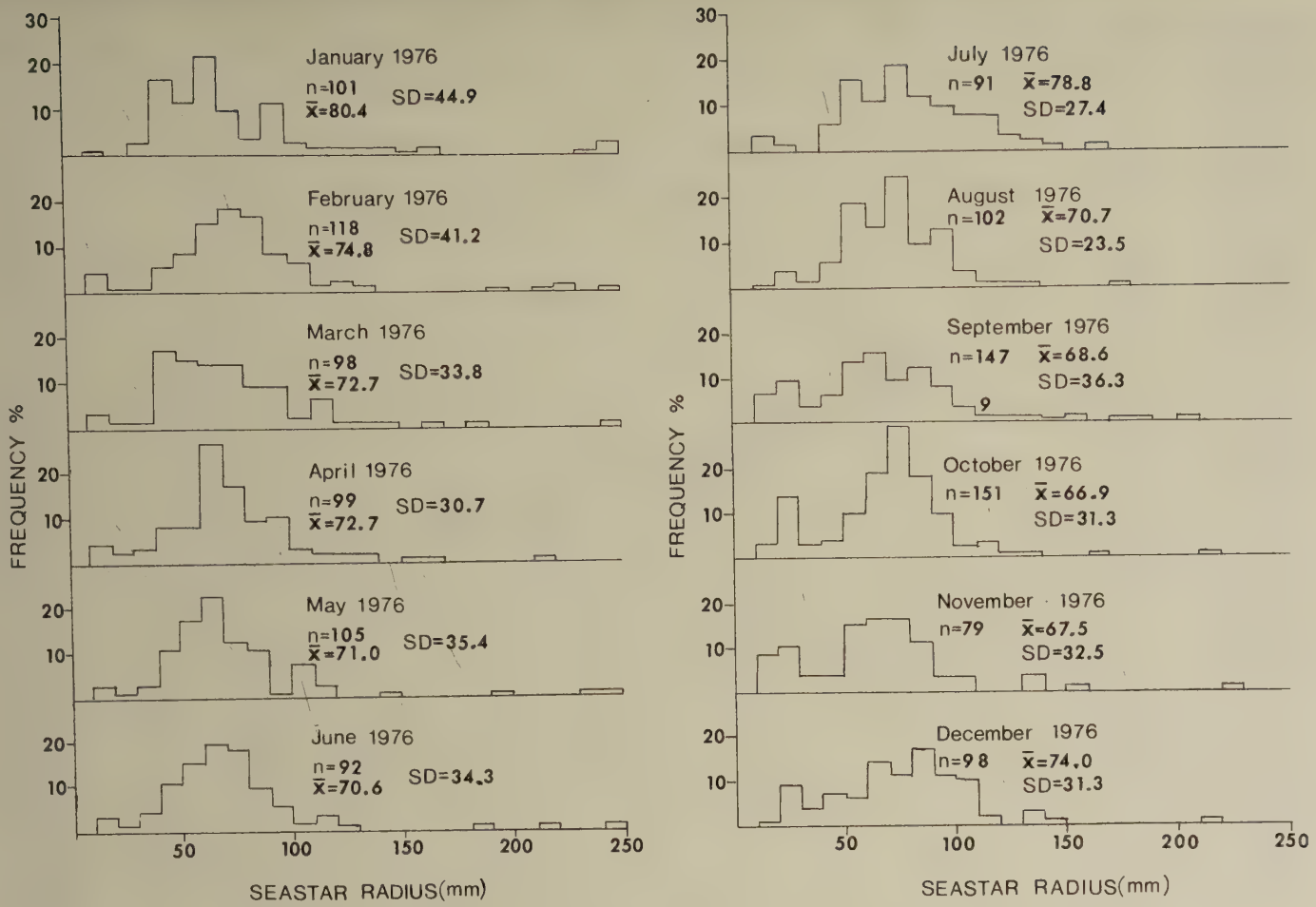

Fig. 8. Size frequencies (%) of intertidal *A. scabra* measured at monthly intervals: *n*, sample size.

the year. Thus, there was a distinctly discontinuous distribution of large and small *A. scabra* in terms of both space and depth. This separation was also based on sexual maturity. The smallest mature seastar encountered in this study had $R =$ 110 mm. Subtidal seastars also had fewer regenerating rays than intertidal specimens (Table II).

Eviscerated wet weight and seastar radius were correlated significantly in intertidal specimens (Fig. 9). Once seastars had reached $R = 110$ mm the eviscerated wet

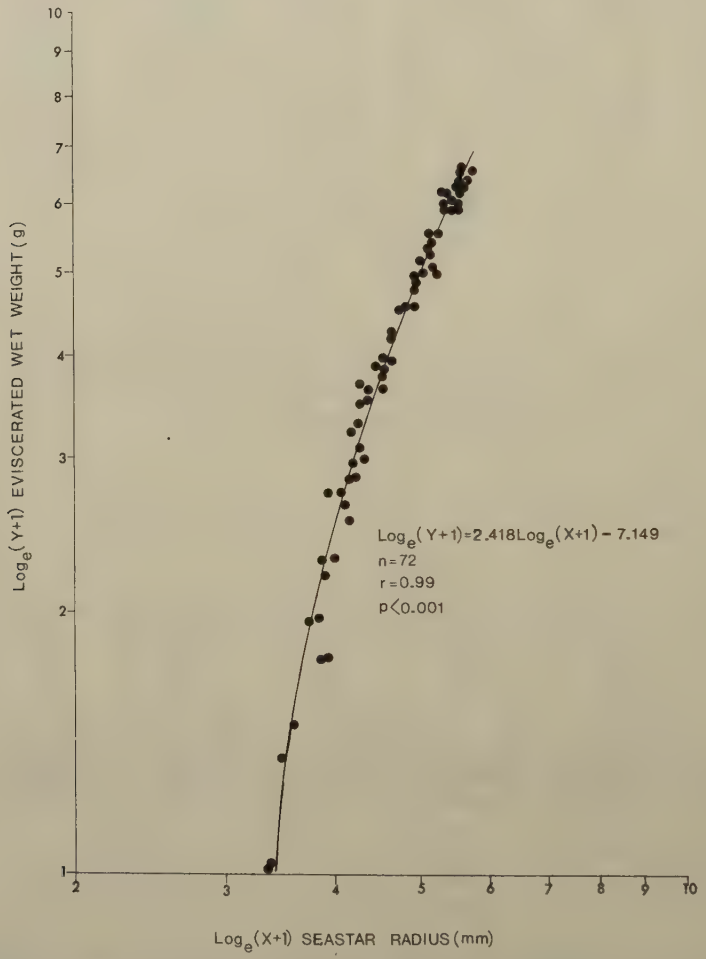

Fig. 9. Relationship between eviscerated wet weight and radius in intertidal *A. scabra*: regenerating seastars omitted.

weight–radius ratios of intertidal and offshore specimens, however, diverged (Fig. 10). For a given radius, seastars taken from depths of 20–146 m were lighter than intertidal individuals (ANCOVA on slope of regression lines in Fig. 10, $F = 7.70$,

$P < 0.01$). *A. scabra* from offshore locations were more liberally supplied with pedicellariae, had lighter pigmentation, and had thinner skeletons than their intertidal counterparts. The latter was the prime cause of the observed differences in size–weight characteristics.

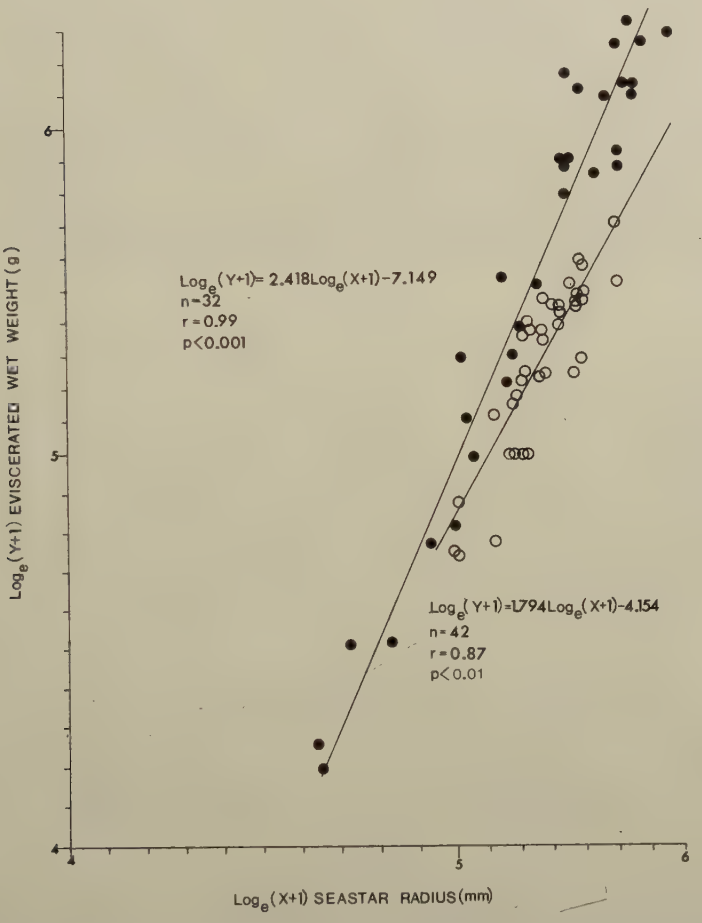

Fig. 10. Relationship between eviscerated wet weight and radius in intertidal (●) and subtidal (○) *A. scabra* exceeding $R = 110$ mm collected in October 1976: regenerating seastars omitted; regression lines compared by ANCOVA (Snedecor & Cochran, 1969).

ANNUAL REPRODUCTIVE CYCLE

In 1975, spawning was between 19 August and 6 September by which time gonad indices had dropped sharply (Fig. 11) and all seastars had small, shrunken gonads. This condition persisted until December, when nearly all remaining gonadal tissue

had been reabsorbed (mean gonad index 0.3). In 1976, gametogenesis (the appearance of new gonadal tissue), commenced in February–March and gonad indices rose gradually until early May. From early May until early June gonad indices rose rapidly and thereafter only a further slight increase was detected. The mean gonad index in June was 13.5, in July 15.8, and in August 15.2. The capability of ova from dissected gonads to be fertilized was checked from March onwards, but successful fertilizations occurred only in June, July, and August. In 1976, *A. scabra* spawned between 28 August and 23 September. Natural spawning was not observed, but the rapid fall in gonad indices suggested that spawning was synchronous and complete. In 1977, spawning was between 25 August and 14 September. During the 3 yr of study, spawning therefore occurred over the same short period from late August–early September. Thus, subtidal ($R \geq 110$ mm) *A. scabra* have a well-defined reproductive cycle and spawn once per year in late winter–early spring.

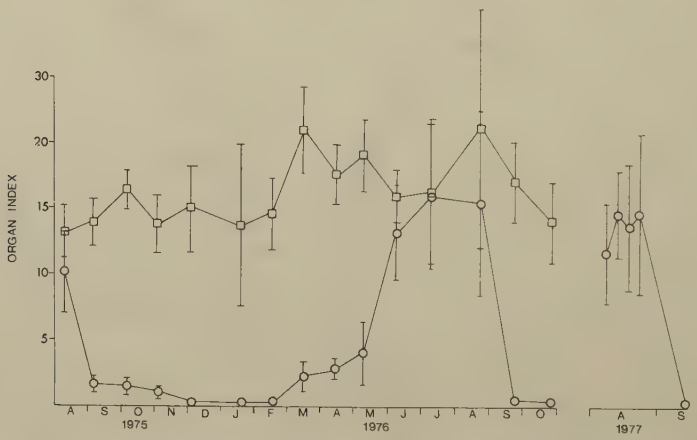

Fig. 11. Mean ($n = 20$) monthly gonad (○) and pyloric caeca (□) indices with 95% confidence intervals for combined male and female *A. scabra* collected from 20–146 m.

Annual gonad index cycles were similar for both males and females with some slight differences in detail (Fig. 12). In 1976, mean female gonad indices rose gradually from March onwards reaching a peak of 19 in late August. Mean male gonad indices also rose gradually from March, but rose rapidly from May to June. The decline in mean male gonad index detected between early July and late August was caused by sample variation, and there was no evidence that males spawned in advance of females.

PYLORIC CAECA INDICES

Although mean pyloric caeca indices varied from month to month, there was little direct correlation with gonad indices. Mean pyloric caeca indices did decline

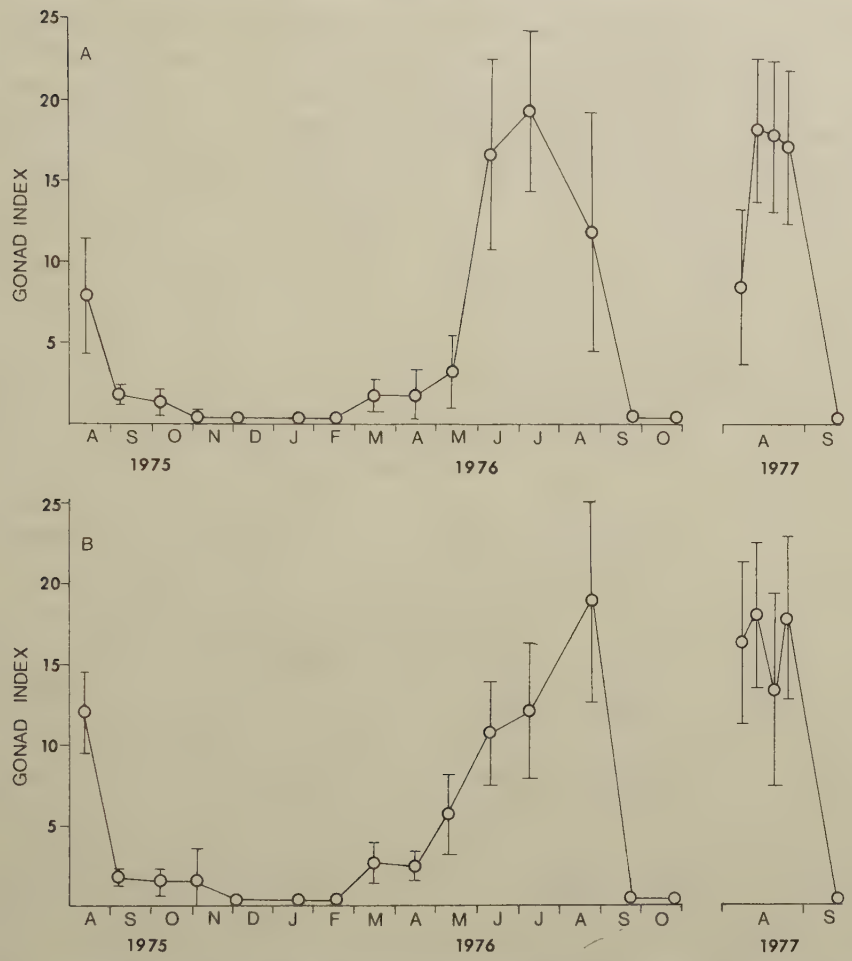

Fig. 12. Mean monthly gonad indices with 95% confidence intervals for male (A, $n = 217$) and female (B, $n = 264$) *A. scabra* collected from 20–146 m.

slightly during the May–June 1976 period of rapid gonad elaboration, and also during the 2 months following spawning (Fig. 11). In neither male, female, intertidal nor sublittoral individuals was there any clear inverse relationship between gonad and pyloric caeca volumes (Fig. 13).

GONAD PRODUCTION

Three factors were found to influence the volume of gonad produced by individual seastars. First, only *A. scabra* of $R \geqslant 110$ mm had measurable gonad volumes and in intact, subtidal *A. scabra* of $R \geqslant 110$ mm the volume of gonad produced by

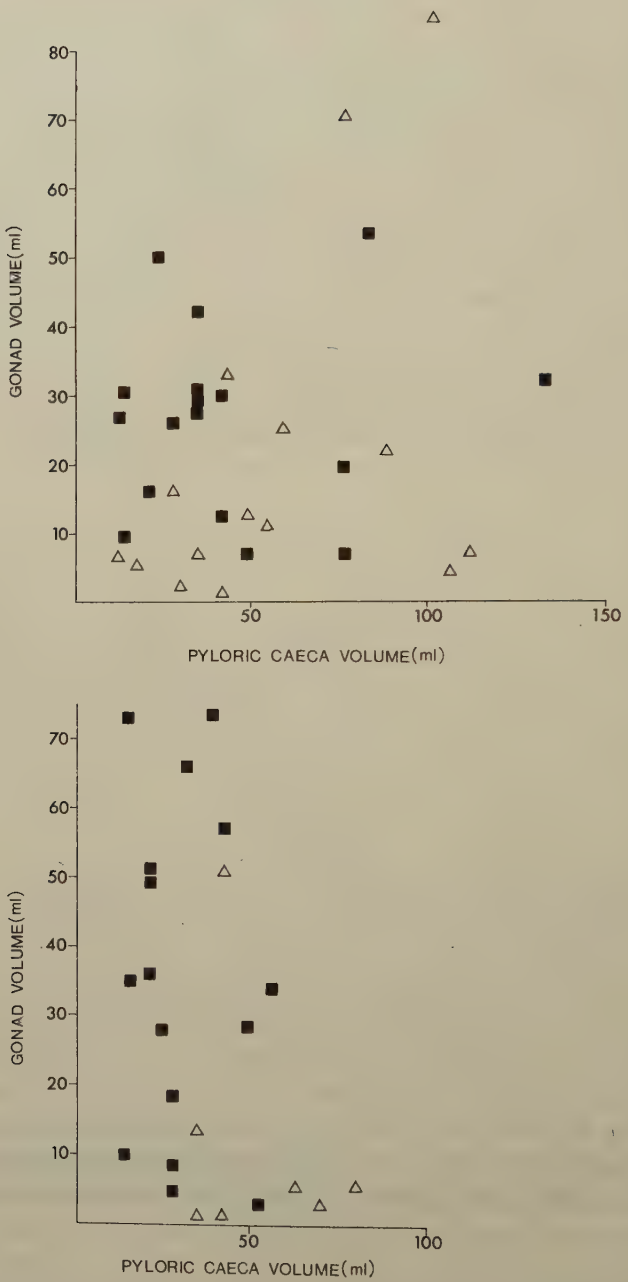

Fig. 13. Relationship between female (upper) and male (lower) gonad and pyloric caeca volumes in subtidal (■) and intertidal (△) *A. scabra* collected in August 1976.

August was significantly correlated with eviscerated wet weight (Fig. 14). This relationship was similar for both males and females (ANCOVA on slope of regression lines in Fig. 14, $F = 0.0005$, $0.05 < P < 0.93$). Secondly, subtidal *A. scabra* which were regenerating damaged rays in August had lower gonad volumes than their intact counterparts. Thirdly, large, thick-skeletoned intertidal seastars had much reduced gonad volumes (Fig. 14).

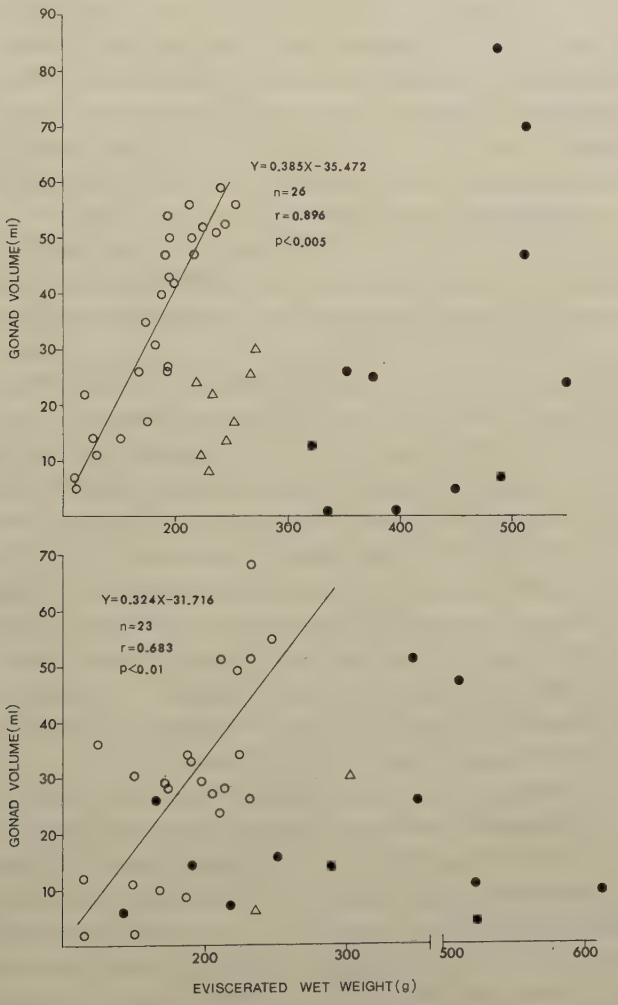

Fig. 14. Relationship between gonad volume and wet weight of eviscerated body in intact subtidal (○), regenerating subtidal (△), and intact intertidal (●) female (upper) and male (lower) *A. scabra* collected in August 1976: regression lines compared by ANCOVA (Snedecor & Cochran, 1969).

Discussion

Net movement of seastars recorded between consecutive searches was additional to a tidal pattern of foraging activity (Town, 1979a). There was no evidence to suggest that seastars returned to a "home base" between foraging periods, nor that they confined themselves within particular limits. Emigrant, immigrant, and resident numbers probably reflected random movement, as seastars displayed little faithfulness to single resting spots, and most individuals remained within a single pool for <30 days (Figs 3, 4). The handling and dyeing of seastars may have induced exaggerated movement and caused increased emigration. At no study sites did seastar numbers exceed 15 during this study. This maximum may have been imposed by the limited number of acceptable under-boulder refuges which, however, were never fully occupied. Alternatively, this might reflect the maximum number of seastars each site can support before overcrowding and competition for food become limiting. No seasonal vertical migration, as noted in other seastars (O'Donoghue, 1924; Mauzey, 1966), was detected. *A. scabra* may exhibit such behaviour in other parts of its geographical range, as movement of this sort varies with latitude (Feder, 1970).

Intertidal (immature) *A. scabra* undertake extensive movement within intertidal and shallow sublittoral zones, but do not venture beyond depths of 20 m. Menge (1975) considered as "nursery areas", or sites of dense larval settlement, two areas in which 68 and 59%, respectively, of *Pisaster ochraceus* were immature. On this basis, the whole of the intertidal zone at Kaikoura could be considered a nursery area as *Astrostole scabra* does not become sexually mature until $R \geqslant 110$ mm (Fig. 14), and only 11.4% of intertidal specimens exceeded this size (Fig. 8). It may be argued that rock-lobster traps, because of their large mesh, did not catch small seastars. *A. scabra*, however, caught in this way clung tenaciously to the bait, and could be moved only with great force, i.e. they did not "drop off" when the trap was raised. Moreover, large seastars of $R = 70$–100 mm, which would have been retained by the mesh, were never caught at depths of 20–146 m.

Bathymetric separation of mature and immature *A. scabra* could be caused by several factors. *A. scabra* may settle only in the intertidal zone and at depths up to 20 m, or seastars which metamorphose in waters deeper than 20 m may be eliminated by predation. Discontinuous spatial distributions of adult and juvenile seastars have been demonstrated by Burla *et al.* (1972) in *Astropecten aranciacus*, and by Doi (1976) in *A. scoparius*, *A. latespinosus*, and *A. polyacanthus*. The causes of this type of separation remain unclear. The quantity or quality of food in the intertidal zone may be incapable of supporting large, reproductive animals, and it is noteworthy that large intertidal specimens had lower gonad indices than subtidal seastars. These large, thick-skeletoned, intertidal individuals may never have migrated offshore, or may have returned to the intertidal zone after a reproductive phase. The constant residence of mature *Astrostole scabra* in subtidal waters may reduce po-

tential intraspecific competition for food and space in the intertidal zone. The relatively increased feeding (immersion) time of offshore seastars probably enhances their reproductive potential through increased food intake. Moreover, reproductive potential is reduced if regeneration is proceeding (Fig. 14) and the incidence and extent of regeneration found in offshore animals was less than that in intertidal *A. scabra* (Table II). Offshore *A. scabra* are less liable to injury by rolling boulders than are intertidal seastars. Some rays could be damaged by some form of attempted predation.

Physical and biotic factors prevailing in the intertidal zone at Kaikoura apparently preclude the residence of *A. scabra* large enough to become mature. That is, if seastars were not to migrate, the mean size of intertidal individuals would stabilize around a value at which immaturity would be sustained. Paine (1976) discovered that subpopulations of *Pisaster ochraceus* had different mean sizes dependent on seastar density and the abundance and type of food present. Furthermore, he suggested that individual seastars might migrate to areas best suited to their metabolic needs. He concluded that a seastar had two options: growth could be adjusted to suit local conditions, or the individual could migrate when its metabolic needs surpassed the ability of the local environment to support them. *P. ochraceus* adjusted its body size, but *Astrostole scabra* of about $R = 110$ mm appear to migrate to deep waters. Some adjustment of body size occurred through the reduction of skeleton thickness once individuals had migrated (Fig. 10), but sexual maturity in *A. scabra* must obviously depend on the abundance and quality of offshore food.

A. scabra spawned over the same short interval in each of the 3 yr studied (Fig. 11). Giese (1959) considered that environmental influences which induce gametogenesis and gamete maturation must act for a more prolonged period than those which trigger spawning. One of the most obvious seasonally variable environmental factors in shallow temperate waters is temperature which, at Kaikoura, rises from October to maxima in January–February (Bradford, 1972). Bradford, however, found no pronounced seasonal temperature variations in waters deeper than 100 m off Kaikoura. As most mature seastars were collected from 20–146 m, it is improbable that temperature alone initiates spawning and gametogenesis.

Spawning in late August–early September is coincident with the spring phytoplankton bloom at Kaikoura which, in the only study conducted in the region (Bradford, 1972), occurred at that time. Logically, asteroids which produce large numbers of planktotrophic larvae should spawn when plankton richness is at a maximum and thereby ensure an adequate food supply for their offspring. Mature ova, capable of being fertilized were present in the ovaries of *A. scabra* from June onwards and female gonad indices did not alter markedly between then and late August (Fig. 12). It is a moot point whether seastars were awaiting an environmental signal or the completion of an endogenous rhythm before spawning. Temperature changes cannot be invoked as an environmental cue as even the shallowest waters in the Kaikoura region undergo relatively little temperature change between late August and early September (Ottaway, 1976).

Mean pyloric caeca indices in *A. scabra* declined during the May–June 1976 period of gonad growth (Fig. 11) but by August 1976 no inverse correlation existed between pyloric caeca and gonad volumes. Mature *A. scabra* did not cease feeding in either immediate pre- or post-spawning periods, and changes in pyloric caeca indices cannot be attributed to such effects. Mature *A. scabra*, almost exclusively restricted to depths of 20–146 m, are unlikely to have temperature-inhibited feeding in winter, and thus show seasonally variable pyloric caeca indices. Similarly, *Pisaster giganteus*, a species restricted normally to subtidal situations, had no seasonally inverse correlation between organ indices (Farmanfarmaian *et al.*, 1958).

Absolute gonad volume in intact, subtidal *Astrostole scabra* was limited by body size (Fig. 14). The peculiar phenomenon whereby regeneration precludes maximum gonad production (Fig. 14) has not been recorded previously for non-fissiparous seastars. Regeneration and gametogenesis might be mutually inhibitory, or the allocation of a portion of energy intake into regeneration may result in the production of fewer gametes. In any case, it is evident that the predominantly subtidal habit of *A. scabra* of $R \geqslant 110$ mm is advantageous in terms of gamete production because the incidence of damage is reduced.

Exactly why *A. scabra* does not develop gonads until $R \geqslant 110$ mm is unclear. Barker (1977) discovered that *Stichaster australis* and *Coscinasterias calamaria* do not mature until $R = 40$ mm and 45–50 mm, respectively. As food-capturing ability in asteroids is improved by increased size (Menge, 1972b), it may be that the diet of small *Astrostole scabra* cannot support growth, self-maintenance, and gonad production. Intact *A. scabra* of $R = 110$–365 mm do occur intertidally, but produce relatively small gonads (Fig. 14). This further implies that intertidal food resources are incapable of supporting substantial gonad development and large size.

A result of the bathymetric separation of mature and immature *A. scabra* at Kaikoura is that small seastars do not compete for food with their larger conspecifics. Menge (1972a) showed that the presence of large *Pisaster ochraceus* maintained small size in *Leptasterias hexactis* which overlapped broadly with respect to diet.

Reproduction in *Astrostole scabra* is typical in that gametes are shed freely and fertilization is external. This mode of reproduction has great potential as a means of dispersal which can reduce local intraspecific competition and allows the rapid location and colonization of food-rich areas. These are important selective agents for large seastars (Menge, 1975).

Acknowledgements

I am grateful to Dr. M. B. Jones, Dr. M. J. Winterbourn, and Professor N. H. Anderson for their constructive criticism of the manuscript. A number of fishermen helped with the collection of subtidal specimens and my wife assisted in the field.

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J. exp. mar. Biol. Ecol., 1980, Vol. 44, pp.133–156
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EFFECTS OF MOONLIGHT ON THE VERTICAL MIGRATION PATTERNS OF DEMERSAL ZOOPLANKTON

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Abstract: The diel vertical migration patterns of demersal zooplankton, those organisms which inhabit bottom substrates but periodically emerge to swim freely in the water column, were determined throughout the lunar cycle. Demersal zooplankton were quantitatively sampled on a subtidal sand flat in the Gulf of California every 2 h for 24-h periods at new, full, first, and last-quarter moons, both as they emerged into the water column and as they returned to the benthos. Demersal zooplankton rarely migrated during daylight. Three general patterns of migration were observed. (1) Polychaetes and cumaceans emerged from the benthos at dusk, regardless of the phase of the moon. Polychaetes returned to the benthos throughout the night while cumaceans returned near dawn. (2) Species of amphipods and isopods exhibited significant avoidance of moonlight, delaying emergence until moonset or returning to the benthos at moonrise. (3) Species of copepods, mysids, shrimp, *Branchiostoma* (cephalochordate), and tanaids emerged into the water column throughout the night. The timing of migration was highly variable and did not correlate with the presence or absence of moonlight. Large zooplankton migrated less frequently into the water column during moonlit periods than small forms, suggesting that nocturnal predation by visually oriented planktivorous fish may be an important selective pressure.

Demersal zooplankton emerged into artificially darkened emergence traps in significantly higher numbers during daylight and during full and quarter moons than into undarkened control traps, demonstrating that absence of light is a major cue stimulating migration. Reentry traps resting on the bottom captured higher densities of demersal zooplankton than either emergence traps or reentry traps suspended off the bottom. Thus, many demersal zooplankton remain near the bottom, rarely swimming far into the water column. Some trap avoidance was observed and current methods for collecting demersal zooplankton are evaluated. Since most demersal zooplankton remained in the water column only a short time, dispersal, particularly over short distances, may be a major advantage of migratory behavior. Migration facilitates rapid recolonization of disturbed or defaunated sites, disrupts and mixes bottom sediments, and results in daily variation in the microdistribution, patchiness, and species composition of the benthic fauna.

INTRODUCTION

Many of the zooplankton found in nearshore marine habitats do not originate in oceanic waters, but rather are resident members of neritic, benthic communities. Two categories of zooplankton are found in close association with the benthos. One category consists of holoplanktonic forms, including various calanoid and cyclopoid copepods, mysids and larval fishes, which swarm near the bottom during the day and disperse into the water column at night (Emery, 1968; Hamner and Carleton, 1979). The second category assumes a benthic mode, living in or directly on the substrate by day. At night these demersal, or bottom-dwelling forms, inclu-

ding various polychaetes, amphipods, isopods, cumaceans, mysids, tanaids, ostracods, copepods, and larvae, move up into the water column. The diel vertical migration of these organisms is a pervasive and long-neglected aspect of nearshore marine communities (Thomas & Jelley, 1972; Alldredge & King, 1977; Porter *et al.*, 1977). Most demersal zooplankton are large in comparison with holoplanktonic forms. In the water column many fall prey to sedentary benthic predators such as corals (Porter, 1974) and to nocturnally foraging fishes (Davis & Birdsong, 1973; Hobson & Chess, 1976).

Since demersal zooplankton emerge from coral reef substrates at night in high densities, it has been suggested that they play an important role in the trophic structure of coral reef communities (Alldredge & King, 1977; Porter *et al.*, 1977). However, it is not only the densities but also the temporal migration patterns of these organisms (i.e., when they enter the water column and how long they remain there) which ultimately determine the availability of demersal zooplankton as food for both pelagic and benthic predators. The emergence of demersal zooplankton primarily at night and the visual orientation of many nocturnally foraging fishes (Hobson, 1975) suggested to us that the timing of migration from the benthos throughout the night may be affected by light levels, particularly moonlight. Previous investigators (Alldredge & King, 1977; Porter *et al.*, 1977) have also speculated that some demersal zooplankton may migrate several times each night, particularly at dusk and dawn. We have quantitatively sampled demersal plankton emerging from and returning to the benthos every 2 h for 24-h periods at new, full, first, and last-quarter moons. Herein we describe the diel migration patterns of the demersal zooplankton resident to a subtidal sand flat and present evidence that light is a major factor governing these patterns.

Methods

Demersal zooplankton were captured on the subtidal sand flat of a protected cove of Danzante Island in the subtropical central Gulf of California, Mexico, during July and August, 1977 and 1978. Samples were collected on a portion of the sand flat approximately 10 m × 10 m in size and 3–5 m deep (depending on the tide) containing uniform coarse-grained sand. Grain size was determined according to Shepard (1963).

Trap design

Cone-shaped emergence traps, 0.25 m^2 at the base, captured zooplankton migrating from the benthos into the water column (Fig. 1). Zooplankton emerging into the traps swam through the 2-cm opening of an inverted funnel, 63 cm above the bottom, and into a removable 4-l polypropylene catch-bottle held in place by surgical tubing. Ninety μm plankton mesh covered the lid of this bottle allowing water

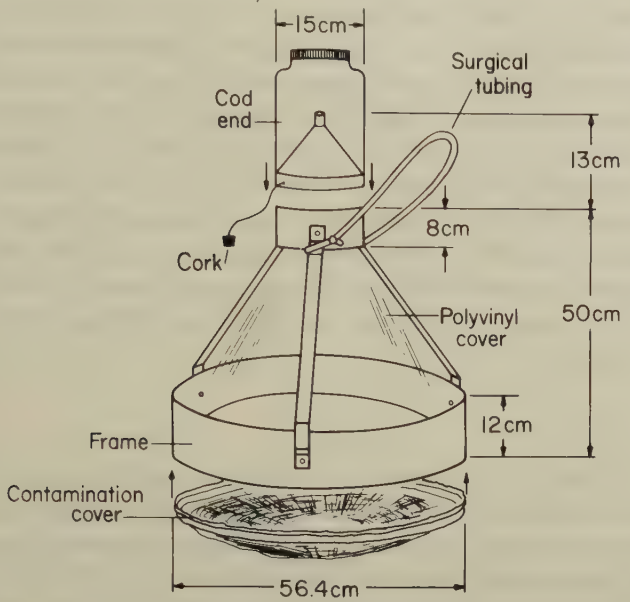

Fig. 1. Diagram of an emergence trap.

exchange with the exterior. Emergence traps were placed on the sand by SCUBA divers. An elasticized cover of 90-μm plankton mesh remained over the base of each trap as it was carried to the bottom eliminating contamination from holoplankton in the water column (Fig. 1). Contamination was further reduced by pushing the stainless steel base of the emergence traps 2–3 cm into the sand, thus forming a gapless seal with the bottom.

Emergence traps inverted to capture animals as they returned to the benthos became contaminated with holoplankton and thus, data based on samples from these traps were not quantitative. Therefore, polyethylene boxes 33 × 22 × 5 cm deep, filled with sun-dried sand from which all the animals had been previously washed, were used to capture demersal plankton returning to the benthos. These reentry boxes were flooded at the surface with 90-μm mesh-filtered sea water, sealed,

TABLE I

The mean percentage (±SD) of demersal plankton remaining in eight sand samples after these had been rinsed 20 times with mesh-filtered water: samples were rinsed 60 times to remove all plankton.

Taxon	Percentage
Copepods	4.4 ± 3.6
Polychaetes	15.3 ± 13.8
Amphipods	2.1 ± 3.0
Isopods	15.4 ± 3.0
Total plankton	4.0 ± 2.3

transported to the benthos and the lids removed during the appropriate sampling period. Later, animals migrating into the boxes were washed from the sand using 20 rinses of mesh-filtered water. Most animals were lighter than the sand and were decanted off with the water. An average of only 4% of the plankton remained in the sand after 20 rinses (Table I). Small, active polychaetes and sphaeromitid isopods, which curl into dense balls, were the most difficult to remove efficiently.

We also tested the efficiency of emergence traps by comparing samples from six emergence traps with six reentry traps placed directly on the bottom and six reentry traps placed 63 cm (the height of the emergence trap funnel opening) above the bottom on a moored rack. Traps were set out near dusk and retrieved the following dawn during full moon.

DIEL EMERGENCE PATTERNS

The density of demersal zooplankton emerging from and reentering the benthos over 24-h periods during new, full, first, and last-quarter moons was monitored for four diel cycles during July and August, 1978. Seven stationary emergence traps and 72 reentry boxes were placed randomly on the study site at 0900. Catch bottles on emergence traps were exchanged, six reentry boxes were closed, and six fresh boxes were opened by SCUBA divers every 2 h. Thus, each reentry box captured plankton returning to the benthos during only one 2-h period of the diel cycle. Divers did not use lights at night and swam carefully to avoid disturbing the sediments. All sampling nights were clear and cloudless. Surface illumination at full moon was 172 lux. Water clarity varied little throughout the study.

Once captured in stationary emergence traps, zooplankton could not return to the benthos again. Thus, the migration patterns of species which entered the water column and returned to the benthos more than once each night could not be detected. We tested for multiple emergence patterns in a separate experiment during 1977, using four emergence traps which were moved carefully to fresh substrates every 2 h throughout four 24-h diel cycles. Only the emergence patterns of those organisms which were regularly or randomly distributed in the benthos could be determined in this manner. Clumped distributions tend to obscure multiple emergence patterns. The distribution of each species across the study site was obtained from previous stationary emergence and reentry trap data and compared with a Poisson distribution using a χ^2 goodness of fit test (Sokal & Rohlf, 1969). All major taxa except polychaetes exhibited marked clumped distributions. The distribution of polychaetes was in agreement with a Poisson distribution. Thus, we could detect multiple emergence patterns with confidence only for this taxon.

EFFECTS OF LIGHT

The effects of light as a cue governing emergence were investigated by covering traps with black polyethylene bags to exclude all light. Six darkened traps and six

control traps covered with clear plastic were set overnight from 1800 to 0700 the following morning during the August full moon in both 1977 and 1978 and from 0700 to 1800 during daylight. Six darkened and six control traps were also set during the last quarter moon in August. Catch-bottles on these traps were exchanged 30 min before moonrise (2300) and retrieved the following morning.

All zooplankton samples were preserved in 4% formalin, counted and sorted to species, and organic weights determined. Samples were filtered onto pre-ashed Whatman GF/C glass fiber filters, dried at 80 °C for 24 h, weighed to the nearest 0.1 mg, ashed at 450 °C for 4 h and reweighed. Preservation results in slight underestimation of ash-free dry weight (Lovegrove, 1966).

Results

The same assemblage of demersal species was consistently captured in both emergence and reentry traps throughout the study period. Amphipods, isopods, polychaetes, and copepods numerically dominated the demersal fauna. Rarer, but ubiquitous, taxa included mysids, cumaceans, tanaids, shrimp, and *Brachiostoma* (cephalochordate). Fish larvae, ostracods, and decapod larvae were captured only intermittently.

DIEL MIGRATION PATTERNS

Migration occurred primarily at night. Fewer than 10% of the total demersal zooplankton migrated into the water column during daylight (Fig. 2). Copepods accounted for most of this migration.

Three major patterns of nocturnal migration were evident: migration at dusk only, migrations correlated with moonlight, and migrations unaffected by moonlight. Differences in the numbers of demersal zooplankton migrating during moonless and moonlit periods of each sampling night were tested statistically using the Mann–Whitney *U*-test (Sokal & Rohlf, 1969). We tested the null hypothesis that the number of zooplankton migrating during any 2-h interval of a moonlit period was equal to the number migrating during any 2-h interval of a moonless period. Each emergence or reentry trap sample was identified as being collected during a moonless or moonlit period and ranked against all other emergence or reentry trap samples collected the same night. Thus, 35 individual emergence trap samples (seven traps sampled at 2-h intervals over a 10-h period) were ranked for each night. Since light conditions remained consistent throughout the nights of full and new moon, we divided these nights approximately in half. Here, 2-h intervals from the first 4 h of the night were ranked against intervals from the last 6 h of the night. If no significant differences were found then we also ranked 2-h intervals from the first

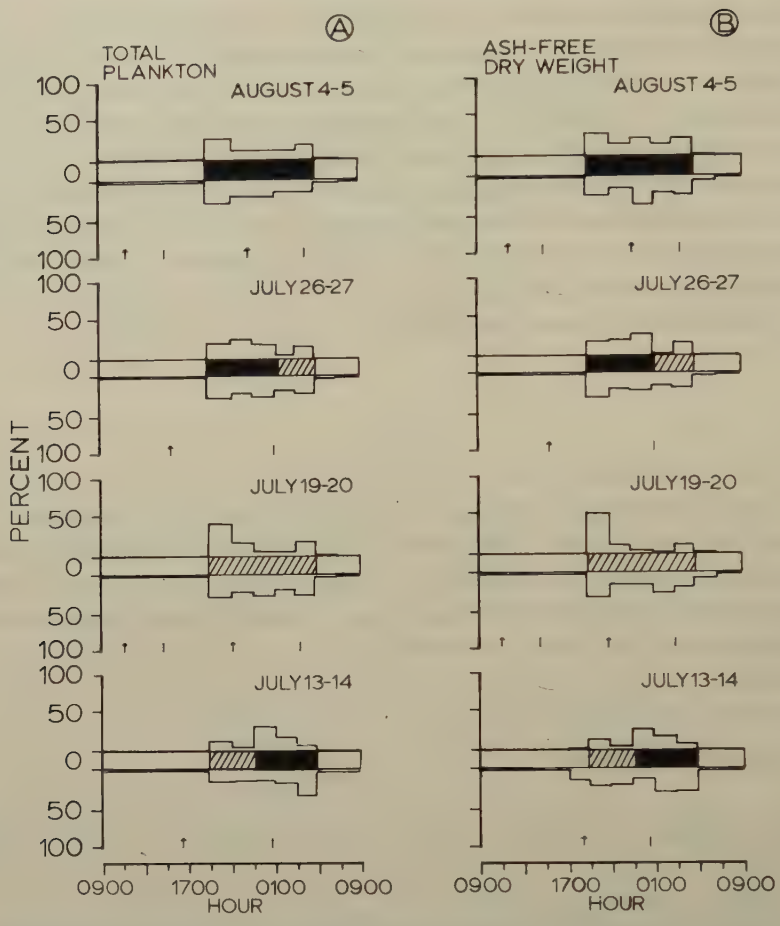

Fig. 2. The migration patterns of the total demersal zooplankton by number (A) and biomass (B) during four diel cycles in 1978: the central, horizontal bar on each graph indicates the light conditions; open bar, daylight; hatched bar, moonlight; black bar, no moonlight; Thus, 4–5 August was the night of new moon, 19–20 July was full moon, etc.; the histogram above the central bar indicates the mean percentage of the total emerging zooplankton population captured in emergence traps during each two hour period of the diel cycle; the histogram below the central bar indicates the mean percentage of the total downward migrating population captured in reentry traps during each two hour period; thus, the timing of migration into the water column (upper histogram) and back into the benthos (lower histogram) is displayed; small arrows below each graph indicate the time of high tide, vertical lines indicate low tide.

6 h against the last 4 h. The migration patterns of all species discussed herein were tested with this procedure.

Migration at dusk

Polychaetes and cumaceans migrated into the water column primarily at dusk.

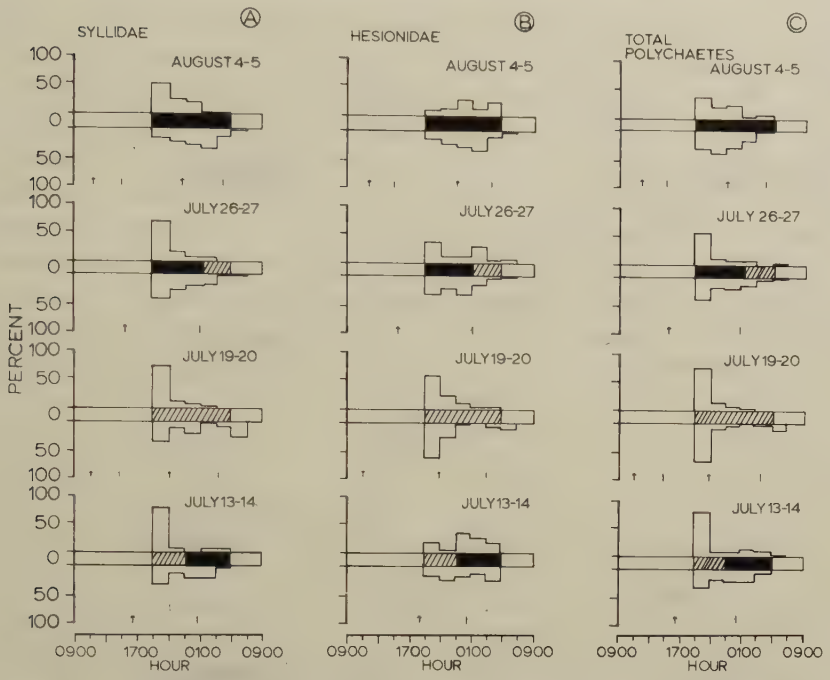

Fig. 3. The migration patterns of Syllids (A), Hesionids (B), and total polychaetes (C): symbols as in Fig. 2.

Polychaetes Polychaetes exhibited the most predictable and inflexible migration patterns, emerging near dusk irregardless of the phase of the moon (Fig. 3). The most abundant polychaetes, *Brainia* sp. and *Sphaerosyllis hystrix* Claparède (Syllidea: Exogoninae) (Fig. 3a) and also *Armandia brevis* Moore (Opheliidae) and *Prionospio heterobranchia newportensis* Reish (Spionidae), emerged from the benthos during the first 2 h following sunset and returned to the benthos throughout the night. *Ophiodromus pugettensis* Johnson and *Gyptis brevipalpa* Hartmann-Schröder (both Hesionidae) also emerged later in the night (Fig. 3b). Four other demersal polychaetes were captured in small numbers: *Protodorvillea gracilis* Hartman (Dorvilleidae), *Pseudoeurythoe* sp. (Amphinomidae), *Nematonereis unicornis* Grube (Eunicidae), and *Aricidea* sp. (Paraonidae).

We tested for multiple emergence patterns in polychaetes by moving emergence traps to fresh substrates every 2 h throughout four 24-h cycles. Polychaetes emerged in large numbers only near dusk, regardless of lunar phase (Fig. 4). Polychaetes apparently migrate into the water column and return to the benthos once each night. Bimodal or multiple emergence patterns were not observed.

Cumaceans Three species of *Cyclaspis*, including *Cyclaspis nubila* Zimmer, and one undescribed species of the genus *Cumella* were demersal. More than 70% of the

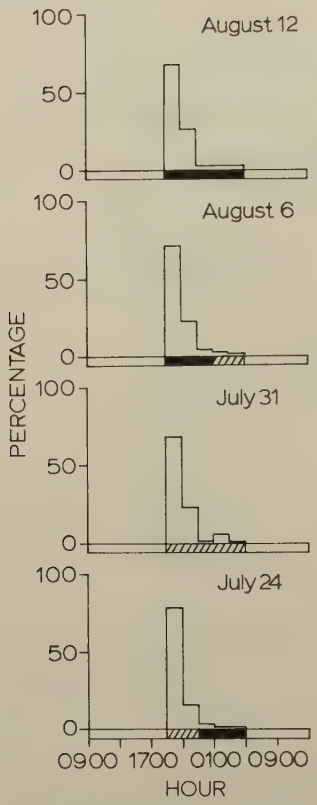

Fig. 4. The timing of the emergence of total polychaetes during four diel cycles in 1977: emergence traps were moved to fresh substrate every 2 h in order to detect possible multiple emergence patterns; symbols as in Fig. 2.

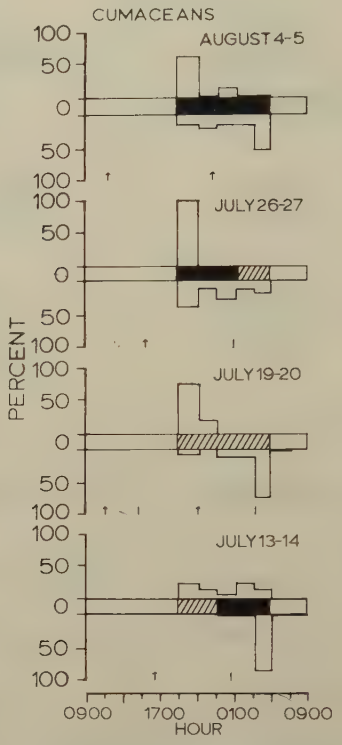

Fig. 5. The migration patterns of cumaceans: symbols as in Fig. 2.

emerging cumaceans migrated into the water column shortly after dusk (Fig. 5), regardless of the lunar phase. First-quarter moon (July 13) was an exception when emergence continued throughout the night. Cumaceans were the only taxon demonstrating a consistent and significant ($P < 0.01$) reentry near dawn (Fig. 5), except during last-quarter moon (July 26). These data indicate that most cumaceans emerge at dusk and remain in the water throughout the night, reentering the benthos near dawn.

Migrations correlated with moonlight

The migration patterns of several major taxa were significantly correlated with lunar phase.

Amphipods We captured 15 species of demersal gammaridean amphipods. The migration of the most abundant species, *Metaceradocus occidentalis* J. L. Barnard, was significantly affected by moonlight. It emerged from the benthos in similar numbers during each 2-h interval of new moon and in high numbers during the first and last intervals of full-moon nights. However, on nights of quarter moons, emergence was significantly higher ($P < 0.01$) during moonless periods, either prior to moonrise or following moonset (Fig. 6a). *M. occidentalis* also reentered the benthos in significantly higher numbers ($P < 0.01$) during the moonless period of first-quarter moon. This is expected since emergence must precede reentry. Similar numbers of *M. occidentalis* reentered the benthos during each portion of the night during new, full, and last-quarter moon (Fig. 6a).

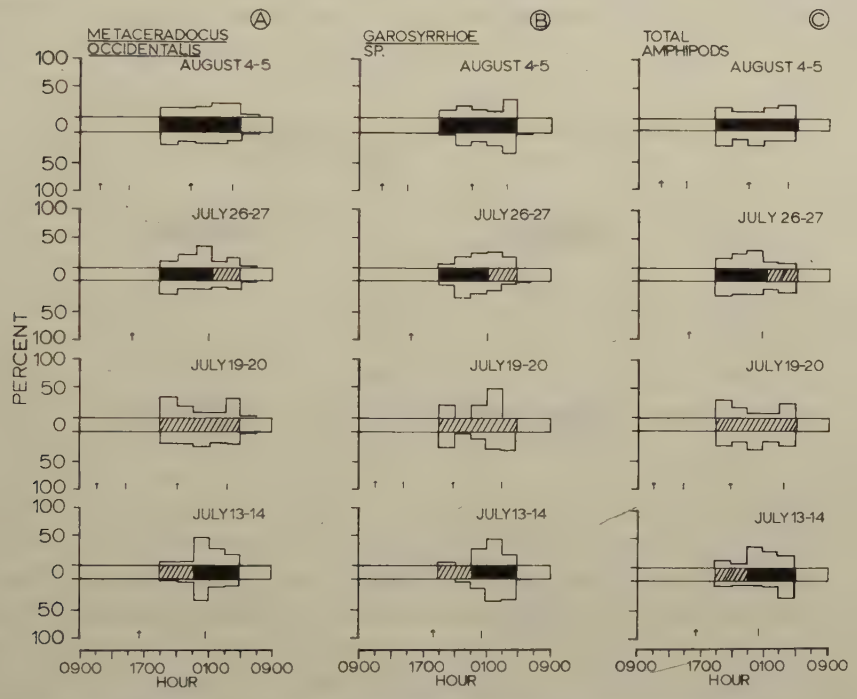

Fig. 6. The migration patterns of abundant amphipods including *Metaceradocus occidentalis* (A), *Garosyrrhoe* sp. (B), and total amphipods (C): symbols as in Fig. 2.

Garosyrrhoe sp. also emerged in significantly higher numbers ($P < 0.01$) during moonless periods of first-quarter moon, delaying emergence until moon set (Fig. 6b). Emergence during the first and second halves of last-quarter, new, and full-moon nights was not significantly different. A similar percentage of the population returned to the benthos during each 2-h period as had emerged during that period. Reentry on the new and first-quarter moons was highest near dawn ($P < 0.01$).

Other amphipods also exhibited significantly higher emergence ($P < 0.05$) during moonless periods of quarter-moon nights, including *Ampelisca cristata* Holmes, *Elasmopus* sp., *Meximaera* sp., *Rudilemboides stenopropodus* J. L. Barnard, *Orchomene* sp., *Lysianassa dissimilis* Stout, and three species of phoxocephalids, including *Platyischonopus viscana* J. L. Barnard, *Foxiphalus* sp., and an unnamed new species and genus (J. L. Barnard, pers. comm.). In general, these species reentered the benthos shortly after they had emerged. Reentry was rarely higher near dawn. Other demersal amphipod species including *Megaluropus* sp. and several species of amphilochids (not identified) did not exhibit patterns of emergence significantly correlated with moonlight.

Fig. 6c summarizes the responses of all demersal amphipods to moonlight. As a general taxon, amphipods emerged from and reentered the benthos in significantly higher numbers ($P < 0.01$) during moonless periods of quarter moons. Although

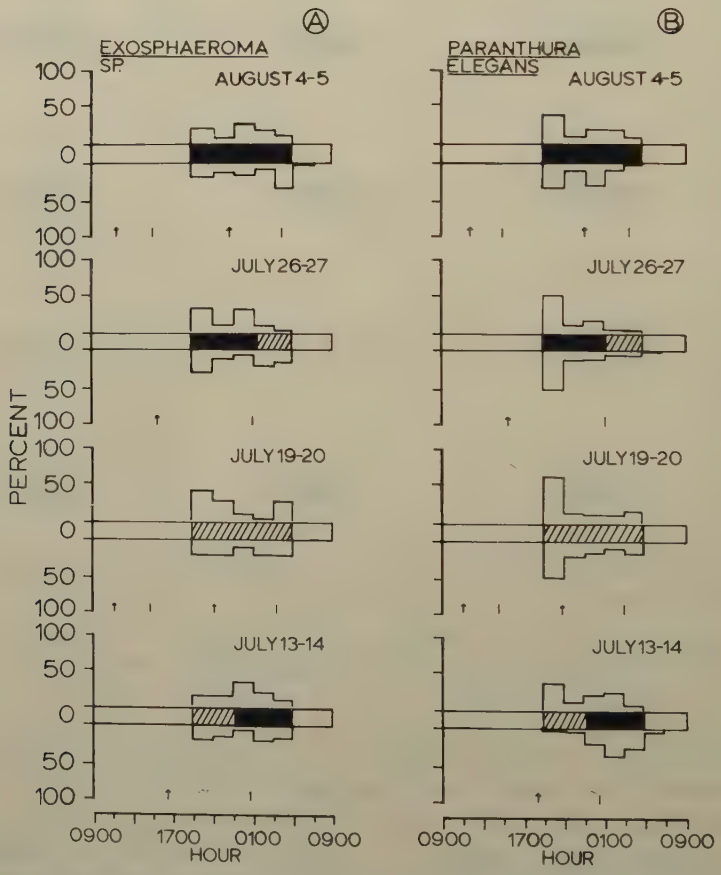

Fig. 7. The migration patterns of the two abundant isopods, *Exosphaeroma* sp. (A) and *Paranthura elegans* (B): symbols as in Fig. 2.

peaks of emergence occurred near dusk and dawn on full and new-moon nights, the number of amphipods emerging was not significantly different during each of those nights. In general, reentry was variable, occurring throughout the night except during first quarter moon when significantly more reentry occurred near dawn ($P < 0.05$).

Isopods A new species of the sphaeromitid isopod genus *Exosphaeroma* and *Paranthura elegans* Menzies were regularly captured in traps. *Serolis carinata* Lockington was also occasionally collected. *Exosphaeroma* sp. exhibited significantly higher emergence during moonless periods of quarter moons (Fig. 7a; $P < 0.01$). Reentry occurred throughout the night. The migration of *Paranthura elegans* was complex. Although significantly greater emergence occurred during moonless periods of last-quarter moon (Fig. 7b; $P < 0.01$), *P. elegans* also exhibited a surge of emergence at dusk on all nights sampled (Fig. 7b). Reentry of *P. elegans* mirrored emergence patterns, suggesting that *P. elegans* remains in the water column only a short time (Fig. 7b).

Migration not correlated with moonlight

The migration of copepods and several miscellaneous taxa were not significantly correlated with lunar phase.

Copepods Demersal copepods were dominated by cyclopoids, particularly *Cyclopina schneideri* Scott. This is the first record of this genus in the eastern Pacific (J. Ho, pers. comm.). Unidentified peltidiid copepods and *Tisbe* sp. (both harpacticoids) were also collected occasionally. Calanoid copepods were rare, comprising less than 5% by number of the copepods collected throughout the study.

Although copepods migrated primarily at night, some emergence occurred during daylight. One to 4% of the copepods migrating during any 24-h period emerged during each 2-h period of daylight (Fig. 8). Significantly higher numbers of copepods emerged at new moon during the first 4 h of darkness (Fig. 8; $P < 0.01$). No significant trends occurred on other nights sampled. Reentry into the benthos was highest during the first hours of darkness on all nights except the first-quarter moon (Fig. 8). There was no clear correlation between the migration patterns of copepods and the phase of the moon.

Miscellaneous taxa Several other taxa were unaffected by moonlight. These included species of *Branchiostoma* (Cephalochordata), an unidentified mysid species, one species of decapod shrimp, and the tanaids *Leptochelia* sp. and *Pancolus californiensis* Richardson. Tanaids also emerged during daylight. Other demersal plankton captured occasionally included a benthic chaetognath (*Spadella* sp.), fish larvae, ostracods, and decapod larvae.

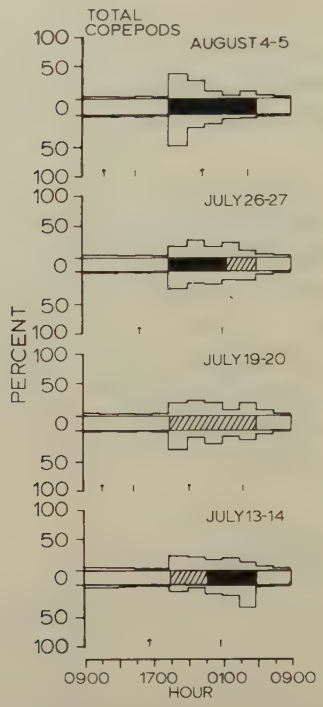

Fig. 8. The migration patterns of total copepods: symbols as in Fig. 2.

Total plankton Fig. 2 summarizes the cumulative migration patterns of the total demersal zooplankton. A significantly higher proportion of the total zooplankton, both by number and ash-free dry weight, avoided moonlight, migrating into the water column during moonless periods of first and last quarter moon ($P < 0.01$). Significantly more zooplankton ($P < 0.01$) also emerged during the first 2 h of full moon. Reentry into the benthos succeeded emergence and was significantly higher during moonless periods of first quarter moon ($P < 0.01$). Reentry during full, new, and last-quarter moons occurred throughout the night (Fig. 2). We could detect no correlations between tidal rhythmicity and migration patterns of demersal zooplankton (see Figs. 2–8).

EFFECTS OF LIGHT

The correlation of the migration patterns of demersal zooplankton with the absence of both daylight and moonlight suggests that decreasing light is a major cue stimulating emergence. We significantly altered the densities of migrating zooplankton and the timing of migration using emergence traps artificially darkened with black plastic covers. Table II summarizes the densities of plankton emerging into darkened emergence traps and into undarkened controls during 11 h of daylight.

Only copepods, amphipods, and tanaids showed substantial daylight emergence in controls. All taxa except tanaids and shrimp emerged into darkened traps in significantly higher numbers (usually an order of magnitude greater) than into controls. Thus zooplankton which did not normally migrate into the water column during daylight could be induced to do so by artificial darkness.

TABLE II

The mean number of zooplankton per m^2 ($\pm$SD) migrating into six emergence traps artificially darkened with black plastic and into six undarkened controls during daylight (0700 to 1700) on 21 July, 1977: the probability that the two treatments were significantly different was determined with the Mann–Whitney *U*-test.

Taxon	Experimental darkened	Control not darkened	*P*
Copepods	1,264 ± 994	178 ± 98	<0.01
Polychaetes	10 ± 5	0	<0.01
Amphipods	194 ± 122	32 ± 32	<0.01
Isopods	230 ± 166	3 ± 3	<0.01
Mysids	8 ± 5	0	<0.01
Cumaceans	2 ± 2	0	<0.01
Tanaids	0	2 ± 2	<0.01
Shrimp	1 ± 1	1 ± 1	>0.2
Total plankton	1,713 ± 1,112	229 ± 140	<0.01

TABLE III

The mean number of zooplankton per m^2 ($\pm$SD) migrating into six emergence traps artificially darkened with black plastic and into six undarkened controls throughout the night of full moon (1800 to 0700 the following morning), 18 August, 1978: the probability that the two treatments were significantly different was determined with the Mann–Whitney *U*-test.

Taxon	Experimental darkened	Control not darkened	*P*
Copepods	4,056 ± 3,099	156 ± 114	<0.01
Syllidae	57 ± 93	79 ± 78	>0.20
Hesionidae	3 ± 7	2 ± 3	>0.20
Total polychaetes	78 ± 98	90 ± 75	>0.20
Metaceradocus occidentalis	3,171 ± 3,269	227 ± 275	<0.05
Total amphipods	3,376 ± 3,330	274 ± 250	<0.05
Exosphaeroma sp.	1,222 ± 740	20 ± 10	<0.01
Paranthura elegans	67 ± 105	8 ± 8	<0.05
Total isopods	1,342 ± 749	28 ± 16	<0.01
Mysids	13 ± 13	0	<0.01
Branchiostoma sp.	8 ± 8	0	<0.01
Cumaceans	3 ± 3	4 ± 4	>0.20
Tanaids	0	3 ± 2	>0.20
Shrimp	9 ± 9	0	>0.20
Total plankton	8,887 ± 2,688	629 ± 293	<0.01

Traps darkened throughout the nights of August full moon also yielded significantly higher densities of demersal zooplankton than undarkened controls. The mean total plankton emerging into darkened traps was more than 10 times greater than the densities collected in controls (Table III). However, migration of some species was not affected by darkening traps. Polychaetes, cumaceans, tanaids, and shrimp emerged into both darkened and undarkened traps in similar numbers (Table III). The migration patterns of these same taxa were unaffected by moonlight during the 24-h sampling studies. The density of total zooplankton emerging into traps darkened during full moon was significantly higher ($P < 0.01$, Mann–Whitney U-test) than the density emerging into traps darkened during daylight.

TABLE IV

The mean number of zooplankton per m^2 ($\pm$SD) migrating into six emergence traps artificially darkened with black plastic and into six control traps throughout the night of quarter moon, 11 August, 1978: the moon was present during the first portion of the night; catch-bottles were exchanged just prior to moonset at 2300 and again after dawn; we tested the null hypotheses (Ho) that the mean number of animals in each taxon in column 1 ($\bar{x}_1$) was equal to the mean of column 3 ($\bar{x}_3$) and the mean of column 3 ($\bar{x}_3$) was equal to the mean of column 4 ($\bar{x}_4$) with the Mann–Whitney U-test.

	Experimental – darkened		Control – not darkened		P	
Taxon	moonlit (1800–2300) 1	moonless (2300–0500) 2	moonlit (1800–2300) 3	moonless (2300–0500) 4	Ho: $\bar{x}_1 = \bar{x}_3$	Ho: $\bar{x}_3 = \bar{x}_4$
Copepods	4,166 ± 3,738	1,606 ± 2,536	431 ± 409	196 ± 192	<0.01	>0.20
Syllidae	10 ± 12	3 ± 3	92 ± 55	0	<0.01	<0.01
Hesionidae	51 ± 51	0	24 ± 13	2 ± 2	>0.20	<0.01
Total polychaetes	64 ± 51	6 ± 7	119 ± 41	2 ± 2	>0.20	<0.01
Metaceradocus occidentalis	3,625 ± 4,246	1,530 ± 1,297	156 ± 50	2,088 ± 1,494	<0.01	<0.01
Total amphipods	3,821 ± 4,372	2,063 ± 1,603	192 ± 96	2,270 ± 1,583	<0.01	<0.01
Exosphaeroma sp.	678 ± 637	326 ± 324	9 ± 9	27 ± 20	<0.01	<0.05
Panthura elegans	106 ± 96	163 ± 98	23 ± 8	25 ± 18	<0.05	>0.20
Total isopods	804 ± 733	490 ± 404	31 ± 10	56 ± 16	<0.01	<0.05
Mysids	14 ± 12	2 ± 2	3 ± 3	7 ± 7	<0.05	>0.20
Branchiostoma sp.	2 ± 2	8 ± 8	0	0	>0.20	>0.20
Cumaceans	5 ± 5	3 ± 3	4 ± 5	2 ± 2	>0.20	>0.20
Tanaids	0	1 ± 1	0	2 ± 2	>0.20	>0.20
Shrimp	2 ± 2	2 ± 2	2 ± 2	0	>0.20	>0.20
Total plankton	9,121 ± 4,812	3,087 ± 2,245	795 ± 400	2,525 ± 1,634	<0.01	<0.05

The results of darkening traps during first-quarter moon in August are summarized in Table IV. Control trap results were consistent with the results of the 24-h sampling studies. The number of migrating copepods, mysids, tanaids, shrimp, *Brachiostoma* sp., and *Paranthura elegans* was not significantly different during moonlit and moonless portions of the night in control traps. However, amphipods and *Exosphaeroma* sp. emerged in significantly higher numbers into control traps

TABLE V

The total mean number of zooplankton migrating per m^2 (±SD) throughout the four 24-h periods of the lunar cycle as measured with both emergence and reentry traps in 1978: *A.*, *Ampelisca*; *M.*, *Metaceradocus*; *G.*, *Garosyrrhoe*; *P.*, *Paranthura*.

Taxon	First-quarter moon 13–14 July		Full moon 19–20 July		Last-quarter moon 26–27 July		New moon 4–5 August	
	Emergence	Reentry	Emergence	Reentry	Emergence	Reentry	Emergence	Reentry
Copepods	353 ± 75	4,522 ± 551	274 ± 58	2,802 ± 306	106 ± 24	2,198 ± 261	273 ± 57	4,430 ± 528
Syllidae	51 ± 12	410 ± 61	53 ± 14	62 ± 23	47 ± 21	148 ± 40	49 ± 15	114 ± 19
Hesionidae	3 ± 3	43 ± 25	77 ± 23	118 ± 38	11 ± 6	82 ± 29	4 ± 3	82 ± 32
Spionidae	1 ± 1	136 ± 62	221 ± 62	146 ± 35	5 ± 2	24 ± 15	3 ± 3	64 ± 25
Opheliidae	3 ± 1	0	2 ± 1	2 ± 2	1 ± 1	3 ± 3	0	0
Total polychaetes	62 ± 14	726 ± 170	358 ± 81	347 ± 65	66 ± 26	285 ± 63	58 ± 18	288 ± 56
A. cristata	2 ± 1	16 ± 8	0	4 ± 3	7 ± 4	10 ± 5	1 ± 1	4 ± 4
M. occidentalis	2,728 ± 899	4,525 ± 719	170 ± 51	4,339 ± 481	559 ± 172	6,296 ± 629	170 ± 48	8,510 ± 1,052
G. disjuncta	40 ± 10	631 ± 107	2 ± 2	273 ± 90	28 ± 12	504 ± 102	18 ± 9	1,074 ± 129
Amphilochids	748 ± 223	3,412 ± 864	29 ± 9	142 ± 41	331 ± 167	699 ± 155	25 ± 13	139 ± 49
Total amphipods	3,894 ± 991	12,199 ± 1,593	266 ± 58	5,342 ± 545	975 ± 291	8,114 ± 690	227 ± 48	10,739 ± 1,108
Exosphaeroma sp.	86 ± 15	1,413 ± 196	6 ± 5	993 ± 152	86 ± 32	695 ± 114	20 ± 10	609 ± 151
P. elegans	198 ± 44	106 ± 35	44 ± 12	112 ± 41	108 ± 30	107 ± 35	90 ± 23	78 ± 32
Total isopods	288 ± 51	1,544 ± 216	50 ± 13	1,131 ± 144	194 ± 53	812 ± 107	111 ± 25	697 ± 155
Mysids	20 ± 9	166 ± 49	19 ± 8	220 ± 74	81 ± 51	134 ± 41	9 ± 5	155 ± 47
Cumaceans	6 ± 4	1,030 ± 321	3 ± 2	120 ± 54	1 ± 1	44 ± 17	15 ± 6	156 ± 64
Tanaids	0	41 ± 15	0	8 ± 8	0	4 ± 4	0	0
Shrimp	1 ± 1	28 ± 20	1 ± 1	19 ± 15	4 ± 3	27 ± 19	2 ± 2	41 ± 23
Branchiostoma sp.	0	4 ± 3	2 ± 1	12 ± 11	3 ± 2	8 ± 5	2 ± 2	23 ± 16
Total plankton	4,678 ± 1,033	20,724 ± 1,933	1,062 ± 141	10,294 ± 658	1,496 ± 377	11,586 ± 1,077	753 ± 119	17,036 ± 1,308
Total ash-free dry weight (mg/m^2)	202 ± 38	1,781 ± 176	63 ± 13	967 ± 100	144 ± 43	1,056 ± 122	38 ± 11	1,605 ± 233

during the later, moonless period. Demersal zooplankton emerged in significantly higher numbers into darkened traps than into controls during the moonlit period of the night. Darkened traps did not increase the density of emerging *Branchiostoma* sp., cumaceans, tanaids, or shrimp during moonlit periods. Syllid polychaetes emerged in significantly lower numbers ($P < 0.01$) in darkened traps than in undarkened controls. This trend was also observed during the full moon (Table III).

ABSOLUTE DENSITIES OF DEMERSAL PLANKTON

Table V summarizes the densities of each major taxon, as determined by both emergence and reentry traps, on the four nights of the lunar cycle discussed previously. Unexpectedly, the absolute densities of animals reentering the benthos, as measured with reentry traps, were an order of magnitude greater than the densities of plankton migrating into emergence traps. We investigated some of the causes of the inconsistency between these two trapping methods by comparing zooplankton captured in reentry traps placed on moored racks 63 cm above the bottom with both emergence traps and reentry traps placed directly on the benthos. Reentry traps moored 63 cm above the benthos captured consistently and significantly fewer zooplankton than did reentry traps placed directly on the benthos, indicating that many zooplankton do not swim high into the water column, but remain near the bottom (Table VI).

Except for amphipods, emergence traps also captured significantly fewer zooplankton than did reentry traps moored at the same height (63 cm) above the bottom. This suggests that some demersal zooplankton may exhibit substantial emer-

TABLE VI

The mean number of zooplankton per m^2 ($\pm$SD) migrating into six reentry traps resting on the bottom (5 cm high), six reentry traps resting on a moored rack 63 cm above the bottom and six emergence traps (funnel openings 63 cm above the bottom) throughout the night of full moon: we tested the null hypothesis (Ho) that the mean of column 1 ($\bar{x}_1$) was equal to the using of column 2 ($\bar{x}_2$) and that the mean of column 2 was equal to the mean of column 3 ($\bar{x}_3$) using the Mann–Whitney *U*-test.

Taxon	Reentry trap height		Emergence trap height	*P*	
	5 cm (1)	63 cm (2)	63 cm (3)	Ho: $\bar{x}_1 = \bar{x}_2$	Ho: $\bar{x}_2 = \bar{x}_3$
Copepods	4,871 ± 878	190 ± 108	24 ± 28	<0.01	<0.01
Polychaetes	904 ± 188	678 ± 146	89 ± 37	<0.05	<0.01
Amphipods	3,331 ± 807	1,703 ± 538	1,723 ± 847	<0.01	>0.2
Isopods	4,650 ± 1096	3,666 ± 691	40 ± 12	>0.2	<0.01
Mysids	5 ± 7	0	0	>0.2	>0.2
Cumaceans	19 ± 11	21 ± 23	2 ± 2	>0.2	>0.2
Tanaids	19 ± 7	18 ± 11	10 ± 4	>0.2	>0.2
Shrimp	7 ± 8	0	0	>0.2	>0.2
Total plankton	13,489 ± 1,841	6,271 ± 873	1,897 ± 846	<0.01	<0.01

gence trap avoidance. However, despite the inconsistent densities of zooplankton captured by the two trapping methods, these methods gave a complementary and consistent picture of the general timing of migration during each night.

Discussion

SAMPLING METHODOLOGIES

The existence and potential significance of demersal zooplankton in near-shore ecosystems has only recently been brought to the attention of marine biologists (Emery, 1968; Porter, 1974; Hobson & Chess, 1976). Three recent studies, one in a Canadian estuary (Thomas & Jelley, 1972) and two on Pacific coral reefs (Alldredge & King, 1977; Porter *et al.*, 1977; Porter & Porter, 1977) present the first quantitative data on the abundance and distribution of these long-neglected organisms. Since these studies have already spawned similar investigations elsewhere (see Randall *et al.*, 1978; Hobson & Chess, 1979) it is essential that potential errors produced by sampling methodologies be promptly recognized. All of these studies deployed various designs of emergence traps giving rise to two possible types of sampling problems; contamination and trap avoidance.

Hobson & Chess (1979) draw attention to the problems of contamination of emergence traps by holoplanktonic organisms, particularly swarming copepods, resident to nearshore communities (see Hamner & Carleton, 1979). They deployed an emergence trap designed to eliminate contamination in an attempt to demonstrate that most copepods in tropical coral reef habitats are not demersal, but rather enter the trap as contaminants. Hobson & Chess (1979) rightly critisize the use of free-floating, tethered traps by Porter *et al.* (1977) and Porter & Porter (1977) which allowed substantial contamination from true holoplankton, particularly copepods, appendicularians, and heteropods. Although Hobson & Chess (1979) discuss contamination arising from cracks a few millimeters in width produced where the rigid Plexiglass traps of Alldredge & King (1977) meet the irregular sea floor over coral, rubble, and rock substrates, they do not point out that the Alldredge–King traps formed gapless seals with the bottom when used over sand substrates. Although sand substrates at Lizard Island on the Great Barrier reef yielded copepod densities 1/10th those of coral and rubble substrates, they still yielded many more copepods than did Hobson and Chess's "contamination-free" traps deployed over sand at Midway and Kure Atolls. Since Hobson & Chess (1979) did not have a control (i.e. a tethered trap), we could conclude that demersal copepods were rare at these locations. The atolls appear to have a lower abundance of demersal zooplankton in general than the Great Barrier Reef. However, a more likely explanation lies in the use of 333-μm mesh plankton netting in the construction of the Hobson–Chess traps. This is a pore size large enough for many of the small demersal copepods we have captured to escape. Our results from the Gulf of California, using

"contamination-free" emergence traps, strongly substantiate Hobson & Chess's (1979) hypothesis that calanoid copepods are rarely demersal. However, our reentry traps which, by design, can capture only plankton burying into or resting directly on the benthos, captured high densities of cyclopoid and harpacticoid copepods (Table V). Many of these copepods do not swim far above the bottom (Table VI) and thus may not be readily captured in emergence traps.

Although trap contamination is an important consideration in quantification and particularly identification of demersal species, a greater source of sampling error may be trap avoidance. Comparisons of emergence and reentry traps placed the same distance above the bottom suggest that some individuals avoid the traps or do not swim into the catch bottle immediately. Amphipods were an exception. An alternative explanation for the disparity between emergence and reentry trap results must be considered. If selection for the clean, uncolonized sand in these traps occurs, reentry traps may overestimate migrating populations. McCall (1977) found that the density of several species colonizing clean mud boxes in the benthos of Long Island Sound was 2 orders of magnitude higher than the natural population densities of those species in the surrounding substrate 10 days after the boxes were first set out. However, Dauer & Simon (1976) found only gradual recolonization of polychaetes, including a demersal species of *Gyptis*, in defaunated benthos. Some demersal plankton, including species of *Ampelisca*, are known to select for areas uncolonized by their own species (Mills, 1967). However, most demersal zooplankton in this study forage in the benthos on meiofauna and detritus. The clean, sun-dried sand initially placed in the reentry boxes would be much lower in food and thus less suitable than the surrounding natural bottom. In addition, each reentry box was open for only 2 h. This is a relatively short time for active selection of the order of magnitude observed to occur.

Reentry traps resting on the bottom apparently capture many individuals which hop or skitter along the surface. Such "hoppers" or "weak swimmers" do not actually enter the plankton and are not readily available to most planktivorous predators. Rather, they are probably preyed upon by demersal fishes and other predators which feed on the substrate surface fauna. Since "hoppers" and "weak swimmers" enter the plankton only momentarily, they are probably best considered as benthic organisms. Emergence traps underestimate the densities of organisms migrating near the substrate. However, they may accurately reflect the densities of true demersal zooplankton available to planktivorous predators because they selectively omit "hoppers" and "weak swimmers". A clear definition of the term "demersal zooplankton" is confounded by our evidence suggesting that different individuals of the same species can exhibit a range of behavior from hopping and weak swimming to sustained swimming in the water column. The behaviour of demersal plankton lies along a continuum between wholly benthic and wholly planktonic animals. The "demersal zooplankton" represent an ecological category for which no clear operational definition may be possible.

It is evident from this study and that of Hobson & Chess (1979) that the methodologies used to sample demersal zooplankton must be carefully evaluated. Underestimation of demersal populations on coral reefs (Alldredge & King, 1977; Porter *et al.*, 1977; Porter & Porter, 1977) and in estuaries (Thomas & Jelley, 1972) may have resulted from trap avoidance. In addition, truly holoplanktonic forms have mistakenly been identified with a demersal habit due to contamination problems in these studies. Despite these problems, emergence traps may be the only practical means of quantitatively sampling demersal zooplankton over some substrate types. Natural coral, rubble or rock substrates cannot be easily recreated in reentry traps. The addition of skirts around the bases of emergence traps deployed over irregular substrates may substantially reduce contamination. However, complete elimination of contamination may not always be possible.

TEMPORAL MIGRATION PATTERNS

Many previous authors have noted the nocturnal vertical migrations of benthic organisms. Williams & Bynum (1972) sampling with nets in the surface waters of North Carolina estuaries captured 58 species of benthic amphipods at night, including species of *Ampelisca*, *Elasmopus*, and *Lysianassa*. Many of these species were most abundant at new or full moon. Polychaetes exhibit well-documented lunar periodicity in spawning at the surface (see Evans, 1971, for review). Species of isopods, including *Exosphaeroma* sp. (Fincham, 1974; Macquart-Moulin, 1976), cumaceans (Anger & Valentin, 1976), copepods (Hart, 1977), and prawns (Hammond & Naylor, 1977) all migrate periodically into the water column.

The onset of darkness is a major environmental cue stimulating emergence of demersal plankton from the benthos. We induced migration during daylight and full moon by artificially darkening traps. Light may be the only cue governing emergence in some species. However, our evidence suggests that other factors work in concert with light in regulating migration patterns. If the onset of darkness were the only stimulus necessary for vertical migration, we expect as many plankton to emerge into traps darkened during the day as when darkened during full or quarter moons. However, many more plankton emerged into traps darkened at full and quarter moon, suggesting that some species may have a circadian rhythm entrained by light. Thus the timing of emergence is not easily changed by disrupting the normal light–dark cycle. Such circadian rhythms have been described in several species of amphipods (MacQuart-Moulin, 1976) and isopods, including *Exosphaeroma* (Fincham, 1974; MacQuart-Moulin, 1976).

Many demersal zooplankton do not migrate every night. Although light may be a major factor governing the timing of emergence during the diel cycle, responses to lunar periodicity and internal motivation factors such as age, sex, or nearness to spawning (Markert *et al.*, 1961; Evans, 1971) or ecdysis (Anger & Valentin, 1976) may ultimately regulate which individuals migrate on any particular night.

We captured the same species in both reentry and emergence traps. Thus, a percentage of each migrating population apparently swims off the bottom far enough to enter the catch bottles of the emergence traps. Since this percentage was not consistent throughout the lunar cycle (copepods were an exception), swimming persistence and vigor may also vary with moonlight conditions and the lunar cycle for many species. Age or sex may also affect the swimming abilities of individual organisms. Female cumaceans, for instance, are weak swimmers compared with males.

Intense predation by visually-oriented diurnal predators has been suggested as the major selective pressure resulting in the vertical migration of demersal zooplankton at night (Hobson & Chess, 1976; Robertson & Howard, 1978). Visually-oriented planktivorous fish are abundant over most benthic communities, including those in the Gulf of California (Hobson, 1965, 1975). Large, highly visible demersal zooplankton migrating during daylight are readily consumed by planktivorous fish. Although squirrelfish (Holocentridae), soapfish (Serranidae), cardinal fish (Apogonidae), grunts (Pomadasyidae), and scads (Carangidae) all forage on small crustaceans and zooplankton at night in the Gulf of California (Hobson, 1965), these fish are less numerous than diurnal planktivores. However, many fish resident over reefs during the day move out to forage over sand flats at night (Hobson, 1975).

Our results suggest that visual predation is a major selective pressure resulting in avoidance of moonlight by many species of demersal zooplankton. We found that large demersal plankton, such as amphipods and isopods, migrate in fewer numbers during moonlit periods. Large species are more easily seen when the moon is bright, and many fish which normally feed during daylight become active on moonlit nights (Hobson, 1965). Thus nocturnal predation pressure may be strongest during moonlit periods. Small copepods and small amphipods (such as the amphilodocids) did not avoid moonlight. These species may be small enough to escape visual detection even when moonlight is present. Many of the polychaetes were large and easily visible, but they migrated primarily at dusk. Twilight is also a period of reduced feeding activity by planktivorous fish (Hobson, 1975).

ADVANTAGES OF MIGRATION

Although selective predation pressure may partially explain the nocturnal timing of the migrations of demersal zooplankton, it does not explain the adaptive advantage of migration itself. Although the advantages of migration may be nearly as diverse as the demersal fauna itself, several major advantages are evident.

Feeding

Some demersal zooplankton may enter the water column to feed. Many of the demersal zooplankton, including shrimp, and some mysids are predatory, possibly feeding on other demersal zooplankton. Cumaceans which remain in the water column throughout the night may also forage there. However, the majority of spe-

cies captured in this study forage in the benthos for food. Several species of *Exosphaeroma* are commensal on bottom invertebrates (Glynn, 1968) and at least one is a selective deposit feeder (Dexter, 1969). Members of the genus *Ampelisca* are tube dwellers feeding primarily on detritus (Mills, 1967). *Orchomene* are benthic scavengers (Thurston, 1979). Many of the amphipods captured here, including phoxocephalids, Lysianassidae and *Megaluropus* sp. are highly adapted for burrowing rather than swimming (Bousfield, 1970) and reentry patterns indicate that they spend little time in the water column.

The polychaetes, *Armandia brevis*, *Ophiodromus pugettensis*, and some syllids are herbivores or deposit feeders (Woodin, 1974; Evans, 1971; Kohn & Nybakken, 1975). The amphioxus, *Branchiostoma* sp., is an indiscriminant suspension feeder (Gosselck *et al.*, 1978).

Reproduction

Synchronous swimming or spawning of polychaetes at the surface is often correlated with lunar cycles (see Clark, 1965; Evans, 1971 for review). The precise timing of the migrations of syllids in this study and the abundance of females carrying eggs suggests that reproduction was occurring. However, many polychaetes take non-spawning migrations to the surface (Clark, 1965). The demersal polychaetes we captured were adults. Sexual epitokes were rare.

Migration patterns of other taxa may also relate to reproduction. Many of the plankton observed exhibit demersal behavior only seasonally during periods of mating and reproductive activity. The amphipod *Ampelisca* swims during certain seasons when sexually mature and mates in the water column (Mills, 1967).

Predation in the benthos

Williams & Bynum (1972) suggested that migrating amphipods avoid intense predation by benthic foragers at night. Hobson & Chess (1976) reject this hypothesis because very few bottom foraging fish are nocturnal. In the Gulf of California, fish, including goat fish (Mullidae), foraged on demersal plankton in the sediments primarily during daylight. However, demersal plankton may escape nocturnal benthic invertebrate predators. Nocturnally foraging gastropods of the genus *Conus* rarely capture syllids on coral reefs even though syllids are the most abundant polychaetes present (Kohn & Nybakken, 1975). These syllids may escape predation through migration into the water column.

Ecdysis

Using SCUBA, Anger & Valentin (1976) directly observed the cumacean *Diastylis rathkei* migrating only during ecdysis at night in the Baltic Sea. Its migration into the relatively safer water column at night results in avoidance of demersal fish

predators during the most sensitive periods of its life; molting, mating, and hatching (Anger & Valentin, 1976). Species of *Cumella* and *Cyclaspis* captured during this study were not undergoing ecdysis, nor did we find discarded molts in our reentry traps. Although demersal plankton may molt in the water column, migration was not related solely to ecdysis.

Dispersal

Migration may promote dispersal of many demersal species to potentially more favorable locations. Several factors support dispersal as a major advantage of demersal behavior. Reentry patterns are often similar to emergence patterns. Approximately the same percentage of plankton return to the benthos during any 2-h period as emerged from it, indicating that emerging individuals remain only a short time in the water column. Dispersal over short distances could be effectively accomplished by only brief migrations into the water column while remaining near the benthos. Mills (1967) suggested that the occasional free swimming of *Ampelisca* allowed ovigerous females to disperse to fresh, uncolonized, and thus unmodified, sediment to release young. Reduced competition between juveniles and adults for both space and food resulted. Demersal behavior would be advantageous for opportunistic species colonizing new habitats particularly if currents carried free-swimming organisms long distances. However, demersal behavior may have the greatest impact on the patchy distributions of species within single habitats. If most demersal zooplankton remain near the bottom and spend a short time in the water column then dispersal will occur over short distances within the same local area. A multitude of factors, including substrate preference (sand grain size, etc.), presence of other colonists, and food availability, must ultimately determine where any particular individual returns to the benthos. Demersal behavior promotes rapid recolonization of disturbed or defaunated sites and produces a mosaic of patches containing different species compositions. We observed marked clumped distributions of most species which supports this suggestion. The species composition and density of these patches and the distribution of the patches themselves changes each night as migration occurs. The effect of demersal behavior on the distribution and ecology of species within benthic communities has not been considered. One important effect in sand and mud bottoms may be the continual disruption and mixing of the sediments from constant migratory activity. Additional studies on the effects of demersal behavior on the microdistributions of benthic organisms are needed.

Acknowledgements

We are particularly grateful to the many who made species identifications, especially J. L. Barnard (amphipods), M. H. Pettibone (polychaetes), R. C. Brusca (isopods and tanaids), R. N. Winn (cumaceans), J. S. Ho (cyclopoids), and R. Ha-

mond (harpacticoids). J. Stretch, J. Purcell, A. M. Wenner, B. Prezélin, S. Career, and C. Ungemach kindly assisted with various aspects of night sampling. This research is partially supported by NSF Grant OCE76-23534.

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J. exp. mar. Biol. Ecol., 1980, Vol. 44, pp. 157–192
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STRUCTURE OF PHYTAL HARPACTICOID COPEPOD ASSEMBLAGES AND THE INFLUENCE OF HABITAT COMPLEXITY AND TURBIDITY

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Abstract: Aspects of the structure (species composition and relative abundance, species associations and interactions, habitat preferences, species diversity and abundance relationships) of phytal harpacticoid assemblages have been investigated from a range of algal types collected in clear (St. Abbs, Berwickshire) and turbid (Robin Hood's Bay, North Yorkshire) waters. A total of over 41 000 harpacticoids were enumerated from eight species of algae at both sites; 10 of the 79 species collected represent new records for the east coast of Britain. The Harpacticidae and Thalestridae contributed 72% of the total fauna and their dominant occurrence supports the concept of geographic parallelism in phytal assemblages. Population densities at St. Abbs were double those at Robin Hood's Bay, but average species diversity (H') over all algae at both sites was similar. Algal species represent quite specific substrata to various harpacticoid species, some of which are morphologically and behaviourally adapted to exploit different algal physiognomies. Significant positive correlations between species were detected and are explained by way of similar substratum requirements and reproductive synchrony; negative correlations relate to reproductive asynchrony and interspecific competition. These features are discussed.

The impact of habitat structural complexity and deposited fine inorganic particulate matter on community variables has been established. A gradient of habitat complexities generated by different species of algae demonstrated how increased micro-spatial complexity allows for significant linearly related increases in harpacticoid species number and diversity. Greater habitable space, increased nutritional resources and reduced levels of predation contribute to this relationship. Smoothing of structural irregularities and the clogging of microhabitat spaces by clay at the turbid site reduces the carrying capacity of harpacticoids and results in significant deviations from the linearity evident in a clear water environment. Log-normal plots of species-abundance data emphasize the predominantly unpredictable non-equilibrium character of phytal assemblages. Ephemeral algae are typified by rapid turnover of opportunistic species, whereas more persistent algae allow an approach to a state of dynamic species equilibrium. A group of species within the Tisbidae is identified as being highly responsive to environmental disturbances resulting in community disequilibrium. Clear water assemblages are suggested to be in a greater relative state of equilibrium than those influenced by turbidity.

Species diversity values from a range of harpacticoid biotopes are presented; the importance of habitat structural complexity is stressed.

INTRODUCTION

The theoretical prediction advanced by MacArthur & MacArthur (1961) that an increase in habitat structural complexity is reflected in concomitant increases in organismic abundance and diversity has now received considerable empirical support from community studies on birds (MacArthur, 1964; MacArthur *et al.*, 1966;

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Karr, 1968; Karr & Roth, 1971, among others), reptiles (Pianka, 1967, 1969), and mammals (Rosenzweig & Winakur, 1969). These demonstrations of vertebrate diversities increasing with vegetational complexity adequately vindicate the prediction, but only recently have attempts been made to apply this same principle to aquatic, and more especially, to marine environments.

Kohn & Leviten (1976) showed how population density and species richness of intertidal assemblages of tropical predatory gastropods was related to topographical features of the shore. More complex habitats allowed for a greater number of species. This effect, moreover, was capable of manipulation by the provision of artificial refuges. In a range of marine habitats Abele (1974, 1976), Spight (1977), and Luckhurst & Luckhurst (1978) working respectively with decapod crustaceans, gastropod molluscs, and coral reef fishes have also linked species richness with substratum heterogeneity. The importance of purely biotically generated topographic complexity has been considered by Heck & Wetstone (1977) and Woodin (1978). The former authors found significant correlations between above-ground biomass of the turtlegrass *Thalassia* and both invertebrate species number and abundance. They regarded higher species richness and density as evolving directly through protection from predators and greater habitable space afforded by higher plant biomass. Similarly, Woodin (1978) provided evidence that environmental disturbances acting to depress diversity may be mitigated by the existence of spatial refuges. Biogenic refuges, or their artificial equivalents, significantly increased species abundance and richness by acting as a buffer to extrinsic mortality or destabilizing processes.

Implicitly then, complex environments present a diverse array of potentially useful niche resources (e.g. attachment surfaces, stratified food reserves) which should be capable of supporting a more diverse array of species and at greater densities. If we regard littoral marine macro-algae as the aquatic equivalent of MacArthur's forest trees, and treat mobile harpacticoid copepods as the parallel of foliage birds, then we are faced with a close analogy within which to view the concept. In a study of phytal harpacticoid assemblages in New Zealand (Hicks, 1977a, b) the composition and number of species and their density was shown in general to be closely tied to the surface area and degree of sediment contamination (see also Dahl, 1948) of the algae investigated. Using these data, but omitting the physically stressed supralittoral site, a rank correlation between number of species and surface area was statistically significant ($P < 0.05$), supporting the proposal that a relationship exists between species richness and complexity of this biogenic habitat. The present paper investigates such relationships further with respect to a variety of community indices. In addition, by comparing two sites with previously demonstrated divergent turbidity regimes, the superimposed impact of inorganic particulate matter on community structure is assessed.

Materials and Methods

AREAS STUDIED

The two sites, Robin Hood's Bay (54°25′N : 0°33′W) and St. Abbs (55°54′N : 2°08′W) on the North Sea coast of Britain were selected because of their different water turbidity regimes. In a thorough investigation of the fauna associated with kelp (*Laminaria hyperborea*) holdfasts in this region, Moore (1972, 1973a) established turbidity criteria along the section of coast from Flamborough Head to St. Abbs Head. Calculated annual mean values of suspended solids showed Robin Hood's Bay ($\log_{10}$ transformed mean dry weight = 1.5180 mg/l, SE ± 0.0497) to be significantly in excess of those for St. Abbs ($\bar{x}$ = 1.1486 ± 0.0171), but this was attributed mainly to the much higher winter values at Robin Hood's Bay ($\bar{x}$ = 1.7366 ± 0.0411), than at St. Abbs ($\bar{x}$ = 1.644 ± 0.0240). The reason for these differences in local turbidity was considered to be the consequence of marine and atmospheric erosional forces on the neighbouring coastal lithologies. Coastal strata at Robin Hood's Bay are soft Liassic shales overlain to sea level by boulder clays. A high tidal range (5 m) means a continuous supply of this material. Wave action along this exposed north-east coast continually resuspends deposited material and it requires prolonged periods of calm weather in summer before significant clarification of the water takes place with correlated contamination of the sea bed (Moore, 1972; pers. obs.). Particle size analysis of a water sample taken at Robin Hood's Bay showed 40% of suspended particles to be fine clays in a diameter range 2–2.5 μm (Shillaker, in Moore, 1978). By contrast, shoreline rocks at St. Abbs are characterized by hard Devonian igneous facies. These are more resistant and are not subject to erosive agencies of such magnitude. There is no justification for believing that conditions have altered since Moore's study; further environmental details can be obtained from his papers.

COLLECTION AND PROCESSING

At both sites, thickly vegetated lower midlittoral pools and shallow sublittoral (< 1 m below L.W.N.) areas were chosen which, as far as shore profile allowed, were comparable in height on the shore and disposition. Sampling levels remained within 1 m in vertical extent so as to minimize possible variability in the fauna caused by tidal level. All algae were submerged at the time of sampling. The selection of algal types was intuitive but was based on earlier criteria (see Hicks, 1977a), to provide a range of physiognomic types offering a range of substratum complexities. Algae selected were: *Ceramium rubrum* (Huds.) C. Ag., *Corallina officinalis* L., *Ulva lactuca* L., *Cladophora rupestris* (L.) Kutz. from lower midlittoral pools, *Fucus serratus* L. and *Palmaria palmata* (L.) O. Kuntze from lower midlittoral channels, and *Gigartina stellata* (Stackh.) Batt. and *Laminaria digitata* (Huds.) Lamour from the sublittoral fringe.

Triplicate samples of each alga were taken from both sites during the same spring

tide period in July 1977. At low water, algae from within a 10 cm × 10 cm quadrat (Hicks, 1977a) were removed directly into plastic bags. Such standardization was difficult with larger thalloid species such as *Laminaria* and *Fucus*, where entire plants were not taken. In these cases the distal portions of fronds fitting within the quadrat were separated from the rest of the plant with a sharp knife. Subsequent comparisons of abundance and composition of mobile harpacticoid fauna from the distal, as opposed to proximal, sections of these algae showed no significant difference (Mann–Whitney *U*-test, $P > 0.05$). This was tested in view of the fact that on phaeophytes some organisms are known to prefer different frond regions (e.g. Ott, 1967; Ryland, 1974; Boaden *et al.*, 1975; pers. obs.).

In the laboratory, the contents of each sample bag were immersed in isotonic magnesium chloride, an effective narcotic for meiofauna (Hulings & Gray, 1971; Hicks, 1977a). Vigorous shaking of algae in this solution has been estimated to dislodge over 90% of the fauna (Hicks, 1977a); 3% formalin was then added to fix the material. The supernatant was filtered through 200-μm plankton mesh after removal of rinsed algal fronds and any larger animals. Algae were retained for determination of their surface area. Samples containing much silt were further "swirl-decanted" (see Hicks, 1977a). Harpacticoids and their copepodite stages were individually hand sorted from graduated Petri dishes, identified, counted and removed for storage in 70% ethyl alcohol.

To test for sample to sample variation a one-way analysis of variance was carried out on the three samples of each alga. At neither site was there a statistically significant difference in the number of species in each sample ($F_{2,21} = 0.154$ and 0.121, $P > 0.25$ for Robin Hood's Bay and St. Abbs, respectively). Representation of individual species was in most cases repeated across the three samples. Species represented by one or two individuals increased variance ratios but at no time did these attain significance. Three samples were thus considered to adequately reflect the fauna from each substratum; sample data were pooled for later faunal and statistical analysis.

Estimation of algal surface area followed the method outlined by Hicks (1977a). One gram of weed, externally dried with acetone, was immersed in a solution of commercial detergent and re-weighed. The increase in weight is directly proportional to frond surface area and was calculated from a standardized regression line (Fig. 6 in Hicks, 1977a); the results of five replicate measurements from Robin Hood's Bay algae are presented in Table I. No difference ($F_{1,14} = 0.045$, $P > 0.25$) was detected from equivalent algae at St. Abbs. Surface area or potential habitable space of the algal substratum is here regarded as a biologically meaningful index of micro-spatial habitat complexity. No corrections have been attempted relating number of species or individuals to a standardized surface area as each alga possesses its own characteristics which were revealed in the raw data and which it was necessary to retain. Significantly more sediment ($t_{15} = 3.90$, $0.005 > P > 0.001$) was deposited on algae at Robin Hood's Bay (Table I).

TABLE I

Surface area estimates of various sampled algae based on five replicate measurements from Robin Hood's Bay: quantities of deposited sediments are based on single samples.

Alga	Detergent weight increases (g) $\bar{x} \pm$ SD	Surface area (cm^2) of 1 g of alga	Dry weight sediment (g)/total algal sample	
			Robin Hood's Bay	St. Abbs
Laminaria	0.045 ± 0.010	7	0.89	0.08
Fucus	0.057 ± 0.022	12	4.2	1.2
Gigartina	0.123 ± 0.086	38	9.4	5.3
Palmaria	0.131 ± 0.037	43	6.9	4.9
Ceramium	0.230 ± 0.071	80	22.3	9.6
Ulva	0.300 ± 0.070	110	5.7	4.1
Corallina	0.341 ± 0.039	120	66.0	29.9
Cladophora	0.568 ± 0.067	216	30.3	12.7

ANALYSIS

Species associations on equivalent algae at both sites and between different algae within the same site were calculated using Czekanowski's coefficient (Sørenson, 1948), i.e.,

$$QS = 2j/(a + b),$$

where a and b are the number of species represented on each alga and j the number of joint occurrences, given double weighting. In all calculations singletons (sensu Clifford & Stephenson, 1975) were omitted for obvious reasons, leading to an objection to this and other non-hierarchical measures, that similarity may approach but never attain the value of unity. Nevertheless, as a qualitative index of faunal similarity, QS was considered adequate for present requirements.

Species diversity was estimated as part of a larger population according to Shannon & Weaver (1963) using the relation,

$$H' = -\sum_{i=1}^{s} pi \log_2 pi,$$

where pi is the proportion of the ith species in the sample. In addition McIntosh's (1967) index was calculated as,

$$MI = 1 - \sqrt{\sum_{i=1}^{s} ni^2},$$

where ni is the number of individuals of the ith species.

The Information function H', while proving to be one of the most robust diversity measures (Heip & Engels, 1974), shows a high correlation with MI ($r = 0.96$, $P < 0.001$, Fig. 1), so that either would have been acceptable here. Given, however, that all indices of diversity have their own inherent mathematical weaknesses (Hurlbert, 1971) and without here proposing to enter this debate, H' is utilized henceforth since it at least allows comparison with previous studies on meiobenthic diversity.

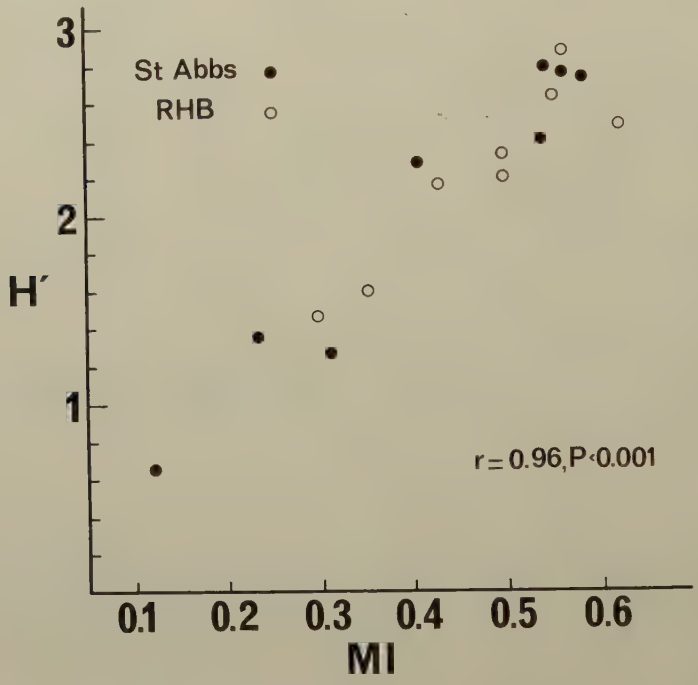

Fig. 1. Relationship between Shannon & Weaver (H') and McIntosh (MI) diversity indices: RHB = Robin Hood's Bay.

In order to examine the two components of diversity, evenness (=equitability) and richness were calculated along with H'. Species richness was derived as $SR = \log_2 S$, and evenness assessed as $J = H'/\log_2 S$ (Pielou, 1966), where S is the number of species.

As a further measure of community structure log-normal plots of species-abundance data were generated following Gray & Mirza (1979).

Aspects of Assemblage Structure

SPECIES COMPOSITION AND RELATIVE ABUNDANCE

A total of over 41 000 harpacticoids were enumerated from algae at Robin Hood's Bay and St. Abbs during this study. Seventy-nine species in 36 genera representing 14 families were identified (Table II), of which two, the Harpacticidae and Thalestridae contributed 72% of the total fauna. These families are amongst those that typify algal communities (Noodt, 1971), so confirming the universal applicability of geographical parallelism in phytal assemblages (see Table 6 in Hicks, 1977b). The Laophontidae was the taxonomically most diverse family with 20 species in seven genera but many species are represented by only one or two individuals.

Table II

Taxonomic composition and relative abundance of harpacticoid families from eight species of algae at Robin Hood's Bay and St. Abbs.

Family	Genera	Species	Individuals (relative abundance)
Harpacticidae	2	6	18752 (0.4484)
Thalestridae	6	16	11296 (0.2701)
Laophontidae	7	20	3507 (0.0839)
Diosaccidae	5	8	2543 (0.0608)
Ectinosomatidae	2	5	2205 (0.0527)
Parastenheliidae	1	1	1468 (0.0351)
Tisbidae	4	7	1122 (0.0268)
Canthocamptidae	1	1	812 (0.0194)
Ameiridae	3	7	59 (0.0014)
Tegastidae	1	1	43 (0.0010)
Peltidiidae	1	3	4 (0.0001)
Longipediidae	1	1	4 (0.0001)
Cletodidae	1	2	2 (0.00005)
Porcellidiidae	1	1	1 (0.00002)
Total	36	79	41818

The total number of individuals of each species and their relative abundance from each site are given in Table III. Ten species are formally recorded for the first time from the east coast of Britain. While there is a non-significant difference in the number of species between the two sites, the algae at St. Abbs support over twice the density of copepods than their equivalents at Robin Hood's Bat ($t_{119} = 10.89$, $P < 0.001$). This largely results from increases in abundance of the commoner species (e.g. *Harpacticus obscurus**, *Zaus spinatus spinatus*, *Parathalestris harpactoides*),

* For taxonomic authorities please see Table III.

TABLE III

List of harpacticoid species recorded from eight species of algae at St. Abbs and Robin Hood's Bay, with total number of individuals and relative abundance: species are ranked according to their intersite totals; previously unpublished new records for the east coast of Britain are denoted by an asterisk.

Species	St. Abbs		Robin Hood's Bay	
	Total individuals	Relative abundance	Total individuals	Relative abundance
Zaus spinatus spinatus Goodsir	4554	0.1628	3869	0.2794
Harpacticus obscurus T. Scott	4617	0.1651	2459	0.1776
Dactylopodia vulgaris (Sars)	2276	0.0814	2589	0.1869
Parathalestris harpactoides (Claus)	2552	0.0913	865	0.0625
Harpacticus chelifer (Müller)	2820	0.1008	100	0.0072
Heterolaophonte longisetigera Klie	2622	0.0938	–	–
Amphiascus "minutus" (Claus)	2394	0.0856	1	0.00007
Thalestris longimana Claus	1050	0.0375	1085	0.0783
Parastenhelia spinosa (Fischer)	1468	0.0525	–	–
Ectinosoma melaniceps Boeck	12	0.0004	976	0.0705
Ectinosoma dentatum Steuer/*californicum* Lang	359	0.0128	503	0.0363
Mesochra pygmaea (Claus)	770	0.0275	42	0.0030
Parathalestris clausi (Norman)	239	0.0086	424	0.0306
Tisbe furcata (Baird)	169	0.0060	365	0.0264
Heterolaophonte strömi (Baird)	463	0.0166	51	0.0037
Ectinosoma normani Boeck	331	0.0118	–	–
Harpacticus littoralis Sars	322	0.0115	–	–
Sacodiscus littoralis (Sars)	146	0.0052	123	0.0089
Tisbe? *minor* (T. & A. Scott)	121	0.0043	118	0.0085
Laophonte setosa Boeck	161	0.0058	5	0.0004
Paradactylopodia latipes (Boeck)	39	0.0014	68	0.0049
Amphiascoides debilis (Giesbrecht)	39	0.0014	53	0.0038
Heterolaophonte denticulata Roe	92	0.0033	–	–
Scutellidium longicauda (Philippi)	68	0.0024	2	0.0001
Laophonte inopinata T. Scott	25	0.0009	29	0.0021
Amphiascus parvus Sars	49	0.0018	–	–
Tegastes clausi Sars*	41	0.0015	2	0.0001
Paradactylopodia brevicornis (Claus)	19	0.0007	13	0.0009
Ameira longipes Boeck	29	0.0010	3	0.0002
Diarthrodes major (T. & A. Scott)	22	0.0008	6	0.0004
Diarthrodes nobilis (Baird)	18	0.0006	6	0.0004
Halectinosoma curticorne (Boeck)	–	–	22	0.0016
Laophonte danversae Hamond	–	–	15	0.0011
Ameiropsis? sp. nov.*	6	0.0002	6	0.0004
Harpacticus septentrionalis Klie*	9	0.0003	1	0.00007
Sacodiscus fasciatus (Norman)	8	0.0003	–	–
Dactylopodia tisboides (Claus)	8	0.0003	–	–
Ameira scotti Sars	8	0.0003	–	–
Diarthrodes aegideus (Brian)*	3	0.0001	3	0.0002
Pseudonychocamptus koreni (Boeck)	6	0.0002	–	–
Laophontopsis lamellifera (Claus)	–	–	6	0.0004
Laophonte foxi Harding	–	–	5	0.0004
Paralaophonte sp. (copepodites)	–	–	5	0.0004
Longipedia helgolandica Klie*	–	–	4	0.0003
Parathalestris intermedia Gurney	4	0.0001	–	–

TABLE III *(continued)*

Species	St. Abbs		Robin Hood's Bay	
	Total individuals	Relative abundance	Total individuals	Relative abundance
Laophonte cornuta Philippi	1	0.00004	3	0.0002
Paronychocamptus curticaudatus (Boeck)	–	–	4	0.0003
Thalestris brunnea Sars	2	0.00007	1	0.00007
Amphiascus tenuiremis (Brady & Robertson)	3	0.0001	–	–
Ameira parvula (Claus)	2	0.00007	1	0.00007
Laophonte serrata (Claus)	2	0.00007	1	0.00007
Normanella minuta (Boeck)	2	0.00007	1	0.00007
Halectinosoma gothiceps (Giesbrecht)	2	0.00007	–	–
Alteutha depressa (Baird)	2	0.00007	–	–
Ameiropsis mixta Sars	–	–	2	0.0001
Heterolaophonte minuta (Boeck)	–	–	2	0.0001
Heterolaophonte littoralis (T. & A. Scott)	1	0.00004	1	0.00007
Ameira minuta Boeck	–	–	1	0.00007
Cletodes tenuipes T. Scott	–	–	1	0.00007
Laophontidae (copepodite)	–	–	1	0.00007
Rhynchothalestris rufocincta (Brady)	–	–	1	0.00007
Alteutha interrupta (Goodsir)	–	–	1	0.00007
Porcellidium 'viride' (Philippi)	–	–	1	0.00007
Harpacticus uniremis Kröyer	–	–	1	0.00007
Paralaophonte spitzbergensis Mielke*	–	–	1	0.00007
Proameira simplex (Norman & T. Scott)	–	–	1	0.00007
Amphiascus c.f. *sinuatus* male Sars*	–	–	1	0.00007
Amphiascopsis cinctus Claus*	1	0.00004	–	–
Tisbe sp., males	1	0.00004	–	–
? *Idyella* sp.	1	0.00004	–	–
Thalestris rhodymeniae (Brady)	1	0.00004	–	–
Paramphiascopsis longirostris (Claus)	1	0.00004	–	–
Dactylopodia c.f. *glacialis* (cop.) (Sars)*	1	0.00004	–	–
Alteutha oblonga (Goodsir)	1	0.00004	–	–
Laophonte thoracica Boeck	1	0.00004	–	–
Heterolaophonte sp., male	1	0.00004	–	–
Thalestris sp.	1	0.00004	–	–
Robertgurneya similis similis A. Scott*	1	0.00004	–	–
Cletodidae (copepodite)	1	0.00004	–	–
Total number of species	60		53	
Total number of individuals	27968		13850	
Total number of species minus singletons	46		36	

rather than loss of rare species. Also at St. Abbs a number of species occur in large numbers which are either not represented in the fauna at Robin Hood's Bay (e.g. *Heterolaophonte longisetigera*, *Parastenhelia spinosa*) or are present but not abundant (e.g. *Harpacticus chelifer*, *Amphiascus "minutus"*). The following 10 species were numerically dominant at Robin Hood's Bay: *Zaus spinatus spinatus*, *Dactylopodia vulgaris*, *Harpacticus obscurus*, *Thalestris longimana*, *Ectinosoma melaniceps*, *Para-*

thalestris harpactoides, *Ectinosoma dentatum/californicum*, *Parathalestris clausi*, *Tisbe furcata*, and *Sacodiscus littoralis*. Dominant at St. Abbs were: *Harpacticus obscurus*, *Zaus spinatus spinatus*, *Harpacticus chelifer*, *Heterolaophonte longisetigera*, *Parathalestris harpactoides*, *Amphiascus "minutus*, *Dactylopodia vulgaris*, *Parastenhelia spinosa*, *Thalestris longimana*, and *Mesochra pygmaea*. These species contributed 95.8% and 89.8% of the fauna at Robin Hood's Bay and St. Abbs, respectively, and may be considered as characterizing the phytal harpacticoid assemblages at the sites investigated. The single most abundant species was *Zaus spinatus spinatus* which accounted for 20.1% of all animals collected from both sites; *Harpacticus obscurus* and *Dactylopodia vulgaris* accounting for a further 16.9% and 11.6%, respectively.

SPECIES ASSOCIATIONS

Czekanowski coefficients using binary (presence–absence) data indicated that the faunal affinity between sites was generally high; the mean *QS* for all algae from both sites is 0.60. Specific *QS* values between sites were: *Ceramium* = 0.38, *Palmaria* = 0.48, *Corallina* = 0.54, *Laminaria* = 0.57, *Cladophora* = 0.60, *Fucus* = 0.67, *Gigartina* = 0.70, and *Ulva* = 0.78. Differences usually involved rarities; dominant components in most cases being repeated. Of the 10 most abundant species from each site, five were shared.

Matrices of faunal affinity between algae within the same site are shown in Table IV. At Robin Hood's Bay the highest degree of inter-algal similarity was between *Ceramium* and *Corallina* which shared 76% of their species, whilst at St. Abbs *Palmaria* and *Ceramium*, and *Ceramium* and *Gigartina* had *QS* values of 0.81 and 0.79, respectively.

TABLE IV

Within site faunal affinity matrices based on Czekanowski coefficients (*QS*): normal type, St. Abbs; italics, Robin Hood's Bay.

	Laminaria	*Fucus*	*Gigartina*	*Palmaria*	*Ceramium*	*Ulva*	*Corallina*	*Cladophora*
Laminaria		0.36	0.37	0.48	0.43	0.32	0.16	0.23
Fucus	*0.70*		0.65	0.65	0.67	0.76	0.46	0.49
Gigartina	*0.48*	*0.69*		0.72	0.79	0.53	0.60	0.52
Palmaria	*0.62*	*0.63*	*0.43*		0.81	0.64	0.47	0.41
Ceramium	*0.40*	*0.65*	*0.60*	*0.42*		0.60	0.53	0.43
Ulva	*0.67*	*0.67*	*0.47*	*0.57*	*0.54*		0.49	0.57
Corallina	*0.29*	*0.50*	*0.61*	*0.30*	*0.76*	*0.40*		0.69
Cladophora	*0.40*	*0.58*	*0.60*	*0.33*	*0.56*	*0.46*	*0.67*	

St. Abbs

Robin Hood's Bay

To determine whether the number of species shared bore any relation to habitat complexity, the percentage of species shared between study site pairs was plotted against surface area. If the kinds of species to be found on a particular substratum were highly predictable then one would expect a significant relation. No such relation was evident ($r = -0.06$, $P > 0.10$), so similarity of habitat complexity simply as measured by the present surface area index does not predict realized similarity in harpacticoid communities. The influence of a number of additional abiotic and biotic factors, including differences in the geographic distribution of component species and biochemical features associated with certain algae, also assumes importance. Different substrata are differently attractive to various species; so relations become complicated. For example, *Ulva lactuca* has been suggested as affecting tidepool organisms by the secretion of metabolic products (Magre, 1974). Such an effect may be selective. The fauna of *Ulva* at both Robin Hood's Bay and St. Abbs consisted largely of tolerant eurytopic species (e.g. *Zaus spinatus spinatus*, *Harpacticus obscurus*, *Dactylopodia vulgaris*, *Tisbe furcata*, *Amphiascus "minutus"*, *Ectinosoma melaniceps*), which presumably are unaffected by *Ulva*'s biochemical exudates. This in consequence boosts the affinity between sites noted for this alga.

Thus, apart from the numerical differences reflected in an analysis of associations, there are some interesting differences in species composition between sites, some of which can be interpreted in terms of micro-habitat differences and corresponding habitat preferences of individual species.

HABITAT "PREFERENCES"

A crude index of habitat "preference" is obtained by tabulating the total abundance achieved by each species over all algae, but perhaps better by the maximum abundance achieved on any one species of alga. This provides an evaluation of the various levels of numerical dominance (McNaughton & Wolf, 1970). Species with a relative abundance $>0.1\%$ are considered here: 19 species from Robin Hood's Bay and 26 from St. Abbs.

The total number of individuals of these species and their mean relative abundance on each alga are given in Table V. There are a number of species which show apparent preferences for specific algae. At both sites *Parathalestris clausi* attained its maximum abundance on *Fucus* where it breeds throughout the year (Hicks, 1979). Some preferred the same alga at both sites, e.g. *Ectinosoma dentatum/californicum* on *Gigartina*, *Paradactylopodia latipes* and *Amphiascoides debilis* on *Corallina* and *Thalestris longimana* on *Ceramium* while others showed intersite differences. At Robin Hood's Bay *Harpacticus chelifer* is at its southernmost limit of distribution on the east coast of Britain (R. Hamond, pers. comm.; pers. obs.) and was found in highest numbers on *Cladophora*, but at St. Abbs it is more abundant on less branched algae. *Mesochra pygmaea* preferred *Gigartina* at Robin Hood's Bay, but *Corallina* at St. Abbs. Other species absent or present only in low numbers on

TABLE V

Total number of harpacticoid individuals on each alga unadjusted for surface area: relative abundance in parentheses; species ranked in order of decreasing abundance, and represent those greater than 0.1% of the intrasite total relative abundances.

	Laminaria	*Fucus*	*Gigartina*	*Palmaria*	*Ceramium*	*Ulva*	*Corallina*	*Cladophora*
Robin Hood's Bay								
Z. sp. spinatus	12 (0.18)	901 (0.53)	518 (0.28)	226 (0.71)	1390 (0.39)	118 (0.64)	461 (0.19)	243 (0.06)
D. vulgaris	20 (0.31)	106 (0.06)	63 (0.03)	4 (0.01)	294 (0.08)	4 (0.02)	532 (0.22)	1566 (0.41)
H. obscurus		13 (0.008)	5 (0.003)		713 (0.20)	3 (0.02)	768 (0.32)	957 (0.25)
T. longimana		7 (0.004)	53 (0.03)		878 (0.25)		93 (0.04)	54 (0.01)
E. melaniceps	2 (0.03)	66 (0.04)	87 (0.05)		51 (0.01)	31 (0.17)	76 (0.03)	663 (0.17)
P. harpactoides		78 (0.05)	515 (0.28)	27 (0.08)	16 (0.005)		122 (0.05)	107 (0.03)
E. dent./calif.	15 (0.23)	19 (0.01)	445 (0.24)	21 (0.07)	1 (0.0003)		2 (0.0008)	
P. clausi	7 (0.11)	374 (0.22)	3 (0.002)		5 (0.001)	2 (0.01)	3 (0.001)	30 (0.008)
T. furcata		51 (0.03)	31 (0.02)	4 (0.01)	132 (0.04)	22 (0.12)	78 (0.03)	47 (0.01)
S. littoralis	7 (0.11)	75 (0.04)	7 (0.004)	33 (0.10)		1 (0.005)		
T. ? minor			88 (0.05)				30 (0.01)	
H. chelifer	1 (0.02)	1 (0.0006)	1 (0.0005)					97 (0.03)
P. latipes					10 (0.003)		57 (0.02)	1 (0.0003)
A. debilis			3 (0.002)		7 (0.002)		34 (0.01)	9 (0.002)
H. strömi					7 (0.002)	1 (0.005)	43 (0.02)	
M. pygmaea			36 (0.02)				6 (0.003)	
L. inopinata			1 (0.0005)				3 (0.001)	25 (0.007)
H. curticorne			1 (0.0005)		4 (0.001)		17 (0.007)	
L. danversae		4 (0.002)			1 (0.0003)		10 (0.004)	
St. Abbs								
H. obscurus			12 (0.004)	4 (0.002)	1018 (0.24)	81 (0.34)	2654 (0.37)	848 (0.11)
Z. sp. spinatus	31 (0.04)	2098 (0.77)	485 (0.16)	1095 (0.60)	673 (0.16)	28 (0.12)	26 (0.004)	118 (0.02)
H. chelifer	757 (0.88)	173 (0.06)	23 (0.008)	662 (0.36)	1201 (0.28)	1 (0.004)	2 (0.0003)	1 (0.0001)
H. longisetigera							58 (0.008)	2564 (0.33)
P. harpactoides		16 (0.006)	1689 (0.56)	21 (0.01)	80 (0.02)	21 (0.09)	697 (0.10)	28 (0.004)
A. "minutus"		3 (0.001)	138 (0.05)	3 (0.002)	3 (0.0007)	12 (0.05)	481 (0.07)	1754 (0.23)

TABLE V *(continued)*

	Laminaria	*Fucus*	*Gigartina*	*Palmaria*	*Ceramium*	*Ulva*	*Corallina*	*Cladophora*
D. vulgaris		39 (0.01)	77 (0.03)	2 (0.001)	267 (0.06)	60 (0.25)	1601 (0.22)	230 (0.03)
P. spinosa							214 (0.03)	1254 (0.16)
T. longimana	1 (0.001)		27 (0.009)	2 (0.001)	1004 (0.23)		15 (0.002)	1 (0.0001)
M. pygmaea			36 (0.01)		1 (0.0002)		650 (0.09)	83 (0.01)
H. strömi						1 (0.004)	130 (0.02)	332 (0.04)
E. dent./calif.	2 (0.002)	2 (0.0007)	320 (0.11)	4 (0.002)	31 (0.007)			
E. normani		1 (0.0004)				11 (0.05)	318 (0.04)	1 (0.0001)
H. littoralis								322 (0.04)
P. clausi		230 (0.08)				3 (0.01)	4 (0.0006)	2 (0.0003)
T. furcata		80 (0.03)	4 (0.001)	3 (0.002)	15 (0.004)	6 (0.03)	29 (0.004)	32 (0.004)
L. setosa							8 (0.001)	153 (0.02)
S. littoralis	64 (0.07)	33 (0.01)	14 (0.005)	25 (0.01)	1 (0.0002)	9 (0.04)		
T. ? minor		1 (0.0004)	19 (0.006)				96 (0.01)	5 (0.0006)
H. denticulata			81 (0.03)	1 (0.0005)	4 (0.0009)		6 (0.0008)	
S. longicauda		49 (0.02)	7 (0.002)	2 (0.001)	10 (0.002)			
A. parvus			45 (0.01)				4 (0.0006)	
T. clausi		3 (0.001)	22 (0.007)	2 (0.001)	2 (0.0005)	1 (0.004)	10 (0.001)	1 (0.0001)
P. latipes				1 (0.0005)			38 (0.005)	
A. debilis			5 (0.002)				31 (0.004)	3 (0.0004)
A. longipes			15 (0.005)		7 (0.002)		7 (0.001)	

other algae at St. Abbs showed high localizations on *Cladophora* (e.g. *Heterolaophonte longisetigera*, *Amphiascus "minutus"*, *Parastenhelia spinosa*, *Laophonte setosa*, *Heterolaophonte littoralis*) while others were concentrated on *Corallina* (e.g. *Ectinosoma normani*) and *Gigartina* (*Parathalestris harpactoides*, *Heterolaophonte denticulata*, *Amphiascus parvus*). *Ectinosoma melaniceps* is most abundant on *Cladophora* at Robin Hood's Bay, while others such as *Tisbe furcata* are substratum generalists at both sites. It is not known whether such intra- or intersite differences in substratum localizations are repeatable and may thus represent true differences in copepod species preference between sites, or whether they reflect some form of forced switch brought about by different niche availabilities, and which reflect the relative abilities of different harpacticoid species to take advantage of such opportunities.

So while there appears to be little pattern of preference for particular algal taxa (i.e. Rhodophyta, Phaeophyta, Chlorophyta), their physiognomy is of great importance. Species increasing in abundance on more branched algae were *Heterolaophonte longisetigera*, *Amphiascus "minutus"*, *Parastenhelia spinosa*, *Dactylopodia vulgaris*, *Mesochra pygmaea*, *Heterolaophonte strömi*, and *Harpacticus obscurus*, while other species were found in highest numbers on flatter, thalloid forms, e.g. *Zaus spinatus spinatus*, *Harpacticus chelifer*, *Sacodiscus littoralis*, *Scutellidium longicauda*. Feeding requirements and morphological considerations are at the root of some of these relations.

Zaus spinatus spinatus, *Sacodiscus littoralis*, and *Scutellidium longicauda* are variously dorso-ventrally flattened and in the last two species the mouthparts and first legs (P1) are so disposed as to form a suction mechanism (also found in *Porcellidium*, another typical phytal genus). They are, therefore, well adapted to broad thalloid substrata with the necessity to resist violent water movements over these bare surfaces. *Zaus spinatus spinatus* is regarded as a "plane sweeper" (B. M. Marcotte, pers. comm.), feeding preferentially on bacteria brushed up by the feeding appendages from planar surfaces. This species is also found in appreciable numbers on "3-dimensional" algae such as *Ceramium*, *Corallina*, and *Cladophora* pointing towards a degree of flexibility in feeding behaviour patterns. *Parathalestris clausi* utilizes mucilage secreted from *Fucus* and, by manipulation with the antennae and other secondary mouthparts, it gathers this, together with associated bacteria, diatoms, blue-green algal, and fungal cells of the Aufwuchs into an aggregate bolus which is then progressively ingested (pers. obs.). This behaviour may be a response to the specific composition of the mucilage and associated flora of *Fucus*, resulting in the observed preference. A similar explanation has been advanced for *Porcellidium dilatatum* which has been shown in experiments (Hicks, 1977d) to actively select another phaeophyte – *Zonaria turneriana*.

Laophontids are poor swimmers and, therefore, require efficient substratum anchoring devices and the added protection of foliose vegetation. The large curved claw on the distal endopod segment of the P1 characterize this family: this, to-

gether with well developed maxillipeds serve as effective grappling hooks with which to embrace fine microhabitat structures such as trichomes, cylindrical branches, and bryozoan zooecia. Together with their demand for rectilinear edges and cylinders from which to feed (B. M. Marcotte, pers. comm.), these features act as powerful restricting agents to distribution. Thus, *Heterolaophonte strömi*, *Laophonte inopinata*, *L. danversae*, *Heterolaophonte longisetigera*, and *Laophonte setosa* attain their highest densities on *Corallina* and *Cladophora* which offer such microstructures and consequent hydrodynamic protection. Moreover, *Heterolaophonte denticulata* and a number of minor species (*H. minuta*, *Laophonte serrata*, *Paralaophonte spitzbergensis*) are preferentially found on *Gigartina* where it is believed they may associate with cheilostome polyzoa such as *Electra pilosa*, commonly found epizooitic on this alga (Ryland & Hayward, 1977). Limited evidence also suggests that *Parastenhelia spinosa* uses its specialized first pair of legs in much the same way as laophontids.

At both sites, *Thalestris longimana* had its distribution centred on *Ceramium*. It is a large species (total length of female $\bar{x} = 1.43 \pm 0.034$ mm SD; $n = 19$), but it is not spatially constrained on *Ceramium* because of the open nature of the interfilament spaces. It uses the robust excavate maxillipeds for grasping. The powerful prehensile claw opposes a ridge on the proximal, densely spinulose inner face of the palm. Although the calculated mean cross sectional diameter of *Ceramium* filaments (measurements made subapically) is nearly twice that of the maxilliped palm area (Mann–Whitney *U*-test; $P < 0.001$), this robust appendage nevertheless allows for a firm grasp. So apart from the short-term use of this alga by *Thalestris longimana* as a place to feed and reproduce (Hicks, 1979), "preference" in this and other instances noted earlier may also be a function of morphological constraint leading in toto to evolutionary adaptation.

SPECIES INTERACTIONS

To test for possible interactions between species, associations of the 10 numerically most important species from each site were determined using Spearman's rank correlation coefficient (r_s) (Tables VI and VII).

Only one significant positive correlation ($P < 0.05$) existed between species from Robin Hood's Bay viz. *Harpacticus obscurus* and *Thalestris longimana*, but significant inverse correlations occurred more frequently. *Zaus spinatus spinatus* was negatively correlated with *Dactylopodia vulgaris* ($P < 0.01$); *Harpacticus obscurus* with *Ectinosoma dentatum/californicum* ($P < 0.05$) and *Sacodiscus littoralis* ($P < 0.01$), while a significant negative correlation also existed between the latter and *Thalestris longimana* ($P < 0.05$).

At St. Abbs, significant positive correlations existed between *Heterolaophonte longisetigera* with *Mesochra pygmaea* or *Parastenhelia spinosa* ($P < 0.01$), and also between the last two species ($P < 0.01$). *Harpacticus obscurus* was positively correla-

TABLE VI

Matrix of Spearman rank correlation coefficients (r_s) of 10 most abundant phytal harpacticoid species from Rob Hood's Bay: – = $P > 0.05$; * = $P < 0.05$; ** = $P < 0.01$.

	Zaus spinatus spinatus	*Dactylopodia vulgaris*	*Harpacticus obscurus*	*Thalestris longimana*	*Ectinosoma melaniceps*	*Parathalestris harpactoides*	*Ectinosoma dent./calif.*	*Parathalestris clausi*	*Tisbe furcata*	*Sacodiscus littoralis*
Zaus spinatus spinatus		−0.93	−0.33	−0.31	−0.36	+0.09	+0.09	+0.12	+0.50	+0.
Dactylopodia vulgaris	**		+0.52	+0.48	+0.24	−0.29	−0.14	+0.26	−0.40	−0.
Harpacticus obscurus	–	–		+0.74	+0.38	+0.02	−0.71	−0.24	+0.50	−0.
Thalestris longimana	–	–	*		−0.14	+0.43	+0.02	−0.48	+0.21	−0.
Ectinosoma melaniceps	–	–	–			−0.07	−0.40	+0.52	+0.07	−0.
Parathalestris harpactoides	–	–	–				+0.60	−0.52	−0.21	−0.
Ectinosoma dent./calif.	–	–	*			–		−0.05	−0.55	+0.
Parathalestris clausi	–	–	–	–	–	–	–		−0.12	+0.
Tisbe furcata	–	–	–	–	–		–	–		−0.
Sacodiscus littoralis	–	–	**	*			–	–	–	

TABLE VII

Matrix of Spearman rank correlation coefficients (r_s) of 10 most abundant phytal harpacticoid species from St. Abb – = $P > 0.05$; * = $P < 0.05$; ** = $P < 0.01$.

	Harpacticus obscurus	*Zaus spinatus spinatus*	*Harpacticus chelifer*	*Heterolaophonte longisetigera*	*Parathalestris harpactoides*	*Amphiascus "minutus"*	*Dactylopodia vulgaris*	*Parastenhelia spinosa*	*Thalestris longimana*	*Mesochra pygmaea*
Harpacticus obscurus		−0.52	−0.69	+0.33	+0.64	+0.64	+0.95	+0.33	+0.24	+0
Zaus spinatus spinatus	–		+0.50	−0.36	+0.02	−0.48	−0.43	−0.52	+0.21	−0
Harpacticus chelifer	*	–		−0.88	−0.36	−0.93	−0.71	−0.62	+0.19	−0
Heterolaophonte longisetigera	–	–	**		+0.19	+0.55	+0.21	+0.99	+0.33	+0
Parathalestris harpactoides	–	–	–	–		+0.36	+0.60	+0.19	+0.43	+0
Amphiascus "minutus"	–	–	**	–	–		+0.60	+0.55	−0.21	+0
Dactylopodia vulgaris	**	–	*	–		–		+0.21	+0.07	+0
Parastenhelia spinosa	–	–	–	**		–	–		+0.33	+0
Thalestris longimana	–	–	–	–	–		–	–		+0
Mesochra pygmaea	–	–	–	**	–		–	**	–	

ted with *Dactylopodia vulgaris* ($P < 0.01$) (Table VII), while *Harpacticus chelifer* had significant negative correlations both with *Heterolaophonte longisetigera* and *Amphiascus "minutus"* ($P < 0.01$), and with *Harpacticus obscurus* and *Dactylopodia vulgaris* ($P < 0.05$).

Significant correlations may be positive, via similar substratum preferences or temporal reproductive synchrony over similar substratum distributions, or negative, via temporal reproductive asynchrony over similar substratum distributions and interspecific competition. Greater abundance of *Heterolaophonte longisetigera*, *Parastenhelia spinosa*, and *Mesochra pygmaea* for purely hydrodynamic reasons on certain preferred substrata, such as the shrubby algae *Corallina* and *Cladophora*, is bound to improve correlations between them. An equally likely explanation for positive correlations may, however, be synchrony of seasonal breeding or protraction of the reproductive season. Since the majority of phytal harpacticoids so far investigated have been shown to breed continuously, or at least over extended periods (Hicks, 1977c, 1979), this explanation seems plausible. Apart from the reproductive cycles of *Zaus spinatus spinatus* and *Parathalestris clausi* on *Fucus* and *Thalestris longimana* on *Ceramium* at Robin Hood's Bay (Hicks, 1979), no published data exist on the breeding patterns in the field of other abundant species represented in this fauna. These species may be used, however, to illustrate the effects of juvenile input on abundance. Both *Zaus spinatus spinatus* and *Parathalestris clausi* breed throughout the year with (usually) more than 30% of adult females carrying eggs at any one time. Copepodites of both species first appear at roughly the same time of year i.e. during late May and early June. Peaks of maximum total population abundance are, however, temporally separated, with *P. clausi* reaching a maximum during the winter and *Zaus spinatus spinatus* attaining highest numbers in early May and late July. Had these abundance relations remained coincidental, significant positive correlations between species would have resulted. In this instance, however, differences between species in the timing of juvenile maxima and population abundance (implying differential growth and mortality rates between them) resulted in a numerical displacement sufficient to yield insignificant correlations. Such relations accord with the theoretical precepts of Huston (1979) who argued that when a community of potential competitors exist under conditions of rapid population growth, the dominant species (which may have a high growth rate or fecundity) would be expected to predominate more rapidly than under conditions where population growth rates of all species were lower. Implied faster growth rates, continuous reproduction and flexibility in food acceptability probably contribute to the success and numerical importance of *Z. spinatus spinatus* in phytal assemblages.

Significant inverse correlations resulting from reproductive asynchrony between species can also be obtained, particularly in species which breed and reach their peak abundance during winter or periods when co-occurring species are at their lowest density. Such an event has been reported for *Amonardia perturbata*, an inhabitant of *Corallina* in Cook Strait, New Zealand (Hicks, 1977c).

Lack of any significant inverse correlation between *Parathalestris harpactoides* and *P. clausi* (Table VI) indicates that they probably do not compete and an examination of their abundance distribution on preferred substrata (Table V) seems to confirm this. But, the significant negative correlation between the two species of *Harpacticus* at St. Abbs (Tables V and VII) is circumstantial evidence that these may compete. No experimental data exist but possible mechanisms of competition would include both exploitative abilities and interspecific interference (Miller, 1967). As food has been suspected as being rarely limiting in phytal biotopes (Hicks, 1977c, 1979), and as *H. chelifer* is the larger more robust species (Table VIII) competition is likely to be for a non-renewable, non-consumable resource (space) and would, therefore, be primarily interference mediated.

TABLE VIII

Size of *Harpacticus* spp. on *Ceramium* at St. Abbs, and matrix of linear ratios based on total length; F = females, M = males.

Species		Total length (mm) $\bar{x}$	Total length (mm) SD	n
H. chelifer	F	1.04	0.083	28
H. chelifer	M	1.09	0.067	27
*H. obscurus**	F	0.59	0.029	20
(small form)	M	0.54	0.026	20
*H. obscurus**	F	0.81	0.024	18
(large form)	M	0.79	0.030	18

1		*H. chelifer*	F	–					
2		*H. chelifer*	M	1.05	–				
3	(small)	*H. obscurus*	F	1.76	1.85	–			
4	(small)	*H. obscurus*	M	1.93	2.02	1.09	–		
5	(large)	*H. obscurus*	F	1.28	1.35	1.37	1.50	–	
6	(large)	*H. obscurus*	M	1.32	1.38	1.34	1.46	1.03	–
				1	2	3	4	5	6

* Confirmed as conspecific by Dr. R. Hamond (Melbourne).

Although the populations of *H. chelifer* and *H. obscurus* are segregated over most algae at St. Abbs there was extensive overlap on *Ceramium* (Table V). The explanation may reside in the rather seasonal occurrence of *Ceramium*. The average duration of sizeable populations of *Ceramium* is about 6–7 months (shorter than the known field longevity of harpacticoids, see Hicks, 1977c) and during its summer proliferation period a number of opportunist species, including *Harpacticus obscurus*, progressively colonize it from other nearby habitats (Hicks, 1979) (see also pp. 181–183). Indeed this is reflected in the low between-site *QS* value (0.38), but high intrasite values (0.76–0.81) indicating that the copepod fauna consists of a range of itinerant species capable of responding to microhabitat expansion and utilizing the short term resources offered by *Ceramium*. This period coincides with what

Wilson (1969) has termed the non-interactive phase, where species in the initial stages of colonizing habitat islands are unaffected by intra- and interspecific interactions. So before competitive displacement has time to operate between *Harpacticus* spp. on *Ceramium*, its annual defoliation either removes resident copepods or alternatively forces them onto other substrata. The extensive coexistence reported is thus only a temporary phase preceding exclusion. Moreover, *Harpacticus obscurus* is represented by two size forms on this alga (Table VIII), with the smaller in the majority. The ratios of size between both forms and between each of these and *H. chelifer* are equivalent to or above Hutchinson's (1959) critical ratio of 1.2–1.4 for congeners (Table VIII), which theoretically allows coexistence whilst removing the need for trophic niche separation. These measurements, however, do not take into account the naupliar and early copepodite stages and it is here that greater overlap through a range of sizes may occur. Habitat and character displacement at present observed on more persistent algae may, therefore, be the outcome of competitive encounters acting through historical sympatry of the early juveniles. This now ensures contemporary intrasite coexistence. As individuals grow the amount of direct competition is reduced as an approach to the "magic" (Horn & May, 1977) size ratio of 1.3 is made. According to Maiorana (1978), complete separation in morphology may generally be necessary to achieve sufficient separation in resource use, because morphological variation is always less than variation in use of a resource. This is particularly so if the resource is spatial. For if the critical resource is food, congeners with a ratio below 1.3 may still be capable of coexistence if behavioural and biochemical differences are sufficient to segregate trophic niches (Ivester & Coull, 1977).

Data are badly needed on dietary components and feeding behaviour before satisfactory conclusions regarding possible nutritional competition can be made. In a personal communication, however, B. M. Marcotte regarded the genus *Harpacticus* as feeding on diatoms, preferentially from flat surfaces ("plane sweepers"). This in his view has the effect of restricting the genus to specialized niches on flat thalloid algae (c.f. a three-dimensional feeder such as *Tisbe furcata*, Marcotte, 1977). In general, habitat distributions support this overview but, while *Harpacticus chelifer* may be considered to have retained this specialized planar feeding mode, *H. obscurus* exploits the three-dimensional cylindrical form of more complex algae.

SPECIES DIVERSITY

Values for species diversity (H'), species richness (SR), and evenness (J) are presented in Table IX together with the total number of species and individuals on each alga from both sites. Average diversity over all algae at Robin Hood's Bay was $H' = 2.23 \pm 0.47$, and was not significantly different from St. Abbs, $H' = 2.04 \pm 0.82$. ($t_7 = 0.643$, $P > 0.50$).

TABLE IX

Community parameters of phytal harpacticoids from each alga at St. Abbs and Robin Hood's Bay.

Habitat	No. of species	No. of individuals	H' $\log_2$	SR ($\log_2 S$)	J ($H'/\log_2 S$)
St. Abbs					
Laminaria	6	858	0.67	2.59	0.26
Ulva	13	239	2.73	3.70	0.74
Palmaria	16	1830	1.27	4.00	0.32
Fucus	17	2733	1.36	4.09	0.33
Ceramium	18	4321	2.42	4.17	0.58
Gigartina	22	3030	2.28	4.46	0.51
Cladophora	32	7789	2.75	5.00	0.55
Corallina	39	7168	2.82	5.29	0.53
$\bar{x}$	20.38	3496.00	2.04	4.16	0.48
SD	10.57	2770.66	0.82	0.83	0.16
Robin Hood's Bay					
Laminaria	8	65	2.49	3.00	0.83
Palmaria	9	318	1.49	3.17	0.47
Ulva	10	184	1.66	3.32	0.50
Fucus	13	1696	2.15	3.70	0.58
Ceramium	19	3521	2.22	4.25	0.52
Cladophora	21	3816	2.34	4.39	0.53
Gigartina	24	1873	2.63	4.59	0.57
Corallina	32	2377	2.89	5.00	0.58
$\bar{x}$	17.00	1731.25	2.23	3.93	0.57
SD	8.49	1471.41	0.47	0.73	0.11

Product-moment correlation coefficients (r; d.f. = 6 in all cases) between H' and log transformed number of individuals were not significant for both Robin Hood's Bay ($r = 0.40$) and St. Abbs ($r = 0.29$), but correlation between H' and log number of species at St. Abbs was significant ($r = 0.75$, $P < 0.05$) while that at Robin Hood's Bay did not quite reach the 5% level ($r = 0.705$). The total number of individuals from each substratum, therefore, contributes little to the calculation of H'. Clearly of more importance is the distribution of individuals between species. This is because when high numbers of individuals were collected in a sample, it was usually the result of the inclusion of a few very abundant species (e.g. *Zaus spinatus spinatus* especially at Robin Hood's Bay, and of *Z. spinatus spinatus* together with *Harpacticus obscurus* at St. Abbs). Species number is thus a better indicator of diversity than total number of individuals.

Evenness (J) was negatively correlated with number of individuals at both Robin Hood's Bay and St. Abbs ($r = -0.49$ and -0.11, respectively), and with number of species at Robin Hood's Bay ($r = -0.26$), but was positively, although not significantly ($r = 0.42$, $P > 0.05$) correlated with species number at St. Abbs. The highly significant correlation of J with H' ($r = 0.91$, $P < 0.01$) at St. Abbs was expected because of the dependence, in part, of J upon H' in the calculation of the diversity index. The correlation of J with H' at Robin Hood's Bay was, however, not significant

($r = 0.50$, $P > 0.05$) but since J is an inverse measure of numerical dominance this would tend to indicate the overall greater equitability amongst individuals at Robin Hood's Bay ($\bar{x}J = 0.57 \pm 0.11$, Table IX). Mean J for St. Abbs is 0.48 ± 0.16. High values of J indicate a lack of dominance and vice versa (compare *Laminaria* from Robin Hood's Bay, $J = 0.83$ where 65 individuals consisted of 8 species, with *Laminaria* from St. Abbs where $J = 0.26$ with 858 individuals consisting of 6 species; the dominant species *Harpacticus chelifer* contributed to over 88% of the total individuals at St. Abbs).

The correlation between SR and the number of individuals was strong ($r = 0.85$, $P < 0.01$) at Robin Hood's Bay but weaker at St. Abbs ($r = 0.75$, $P < 0.05$), and suggests that the more individuals added to the samples increased the likelihood of obtaining additional species. These correlations were not reflected in those between H' and number of individuals or between J and number of individuals, because H' and J also reflect the distribution of individuals. High total numbers of individuals are usually associated with inequalities of the common species.

TABLE X

Regression equations of phytal harpacticoid community parameters: H' = Shannon & Weaver diversity; J = Pielou evenness; $SR = \log_2 S$ number of species; $N = \log_e$ number of individuals; all plotted against $\log_e$ surface area (x) of eight species of algae from both St. Abbs and Robin Hood's Bay.

$y = a + bx$	r	P
St. Abbs		
$H' = -0.4164 + 0.6318 \log_e x$	0.908	$P < 0.01$
$J = 0.5505 + 0.1088 \log_e x$	0.795	$0.02 > P > 0.01$
$SR = 2.1743 + 0.5119 \log_e x$	0.731	$0.05 > P > 0.02$
$N = 6.6217 + 0.2894 \log_e x$	0.291	$P > 0.10$
Robin Hood's Bay		
$H' = 2.2776 - 0.0113 \log_e x$	−0.028	$P > 0.10$
$J = 0.8269 - 0.0655 \log_e x$	−0.694	$0.10 > P > 0.05$
$SR = 2.5851 + 0.3456 \log_e x$	0.556	$P > 0.10$
$N = 4.1702 + 0.6741 \log_e x$	0.521	$P > 0.10$

The significance of algal foliage complexity in determining harpacticoid diversity has been established with regression analyses of St. Abbs and Robin Hood's Bay data (Table X). Regression lines of H' and J were plotted for each site in Fig. 2; analysis of covariance confirms the visual impression of a highly significant ($P < 0.001$) difference in slope between both sets of data. At St. Abbs H', J, and SR were all positively correlated with increasing complexity of algae as estimated by the surface area method. Variations in habitat complexity account for 82% of the variations in H', and 53% of the variations in number of species (Table X), again emphasizing the importance of species number in determining H'. A relation of the number of individuals with surface area was not significant ($r^2 = 0.08$). So in

contrast to diversity, density is poorly correlated with habitat complexity; this result was anticipated from the raw data as a few species can form dense populations on less complex algae, e.g. *Fucus*, *Laminaria*.

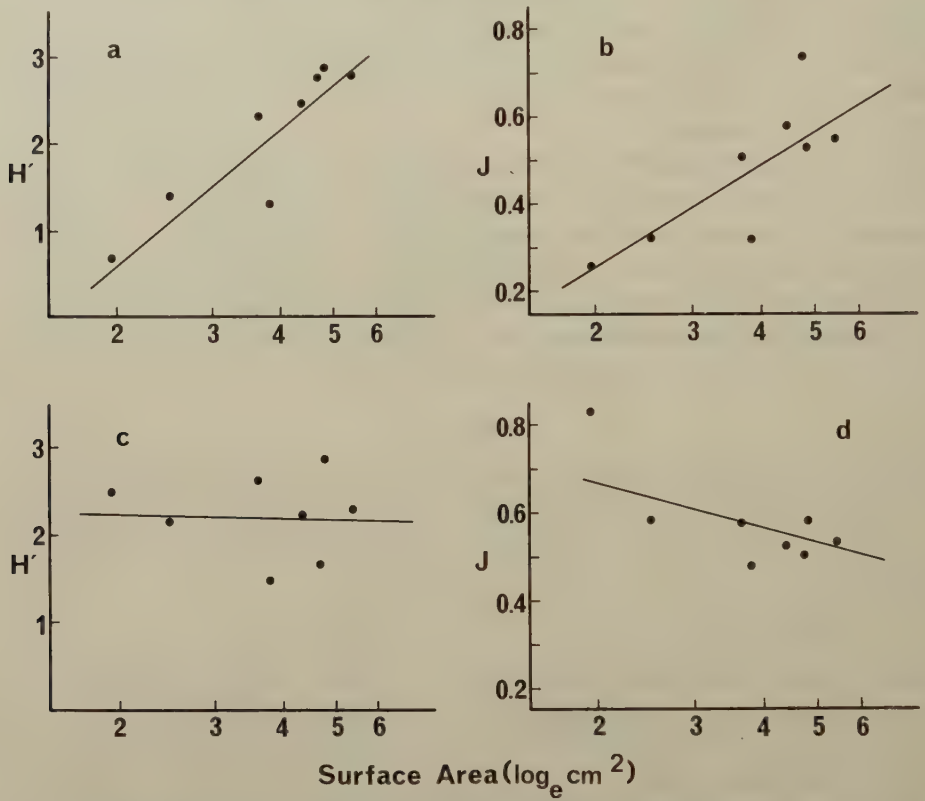

Fig. 2. Relationship of phytal harpacticoid community parameters H' (Shannon & Weaver diversity) and J (Pielou evenness) with habitat complexity (surface area of algae) at a clear water site (St. Abbs, a and b) and a turbid site (Robin Hood's Bay, c and d).

At Robin Hood's Bay, diversity was inversely correlated with complexity although this relation was not significant ($P > 0.10$); variations in complexity accounted for 48% of the variations in J but these were also not quite significant at the 5% level. Relations of SR and N were likewise not significant. The Robin Hood's Bay data, therefore, have a large residual variance compared with data from St. Abbs. It is suggested that this variance is accounted for by the influence of inorganic particulate material, to be discussed in more detail later.

Diversity values from the present study have been compared with other harpacticoid assemblages ranging from intertidal to deep-sea environments (Table XI). Strict comparability is unattainable because of methodological and biotopic differences and different logarithmic transformations used in calculation of H'. Despite

TABLE XI

Summary of maximum obtained species diversity (H') values based on a range of harpacticoid assemblages: values have in some cases been calculated from tabulated species abundance data, here denoted by an asterisk.

Substratum	Depth (m)	No. of samples (n)	Maximum H'	Reference
Sand-silt	13	48	3.9	Coull (1970)*
Mud	? bathyal	10	3.3	Drzycimski (1969) given in Hartzband & Hummon (1974)
Silt-clay	3000	1	4.54	Coull (1972)
Laminaria holdfast	1–5	5	5.17	Moore (1973b)*
Coarse sand	3.1	1	3.3	Hartzband & Hummon (1974)
Mud	16	3	2.5	Marcotte & Coull (1974)
Sand	1	4	2.2	Coull & Fleeger (1977)
Ecklonia fronds	6	24	4.07	Hicks (1977b)*
Silt	1220	14	4.2	Thistle (1978)
Fine sand	intertidal	2	3.38	Moore (1979)
Corallina fronds	0.2	3	2.89	present study

these limitations certain conclusions can be drawn. The highest diversities so far recorded are in algal holdfast communities, but the deep-sea and shallow-water algal frond assemblages also yield high values. Moore's (1973b) re-calculated holdfast data ranged from $H' = 2.4$ at Robin Hood's Bay to 5.2 at Beadnell, and gave a mean diversity over 15 sites of 3.81 ± 0.689 SD; 12 months samples from *Ecklonia radiata* fronds in Cook Strait (Hicks, 1977b) yielded a value of H' of 4.1. Coull's (1972) values (Shannon H' values obtained as a separate from the author) ranged from 3.62 at a 1020-m station to 4.54 at a 3000-m station representing the highest deep-sea diversities yet attained. Moreover, evenness (J) values in depths >500 m ranged from 0.84 to 0.93 emphasizing an extreme lack of dominance in deep-sea assemblages, which contrasts sharply with shallow-water and algal communities.

SPECIES-ABUNDANCE RELATIONS

Gray (1978) and Gray & Mirza (1979) have suggested that multispecies meiofaunal communities conform to a log-normal distribution (Preston, 1948) derived by plotting the number of species against the number of individuals per species on a geometrical scale. This method is used here where the cumulative percentage of species is plotted on a probability scale against the number of individuals divided into octave ($\times 2$) log classes. Such plots can be regarded as graphical representations of sample evenness (Edden, 1971). A good fit to a log-normal model gives a straight line (irrespective of slope). Such a community may be considered to be in an equilibrium state where immigrants balance emigrants (MacArthur & Wilson, 1967) and the proportion of individuals per species remains fairly constant (Gray & Mirza, 1979). Depar-

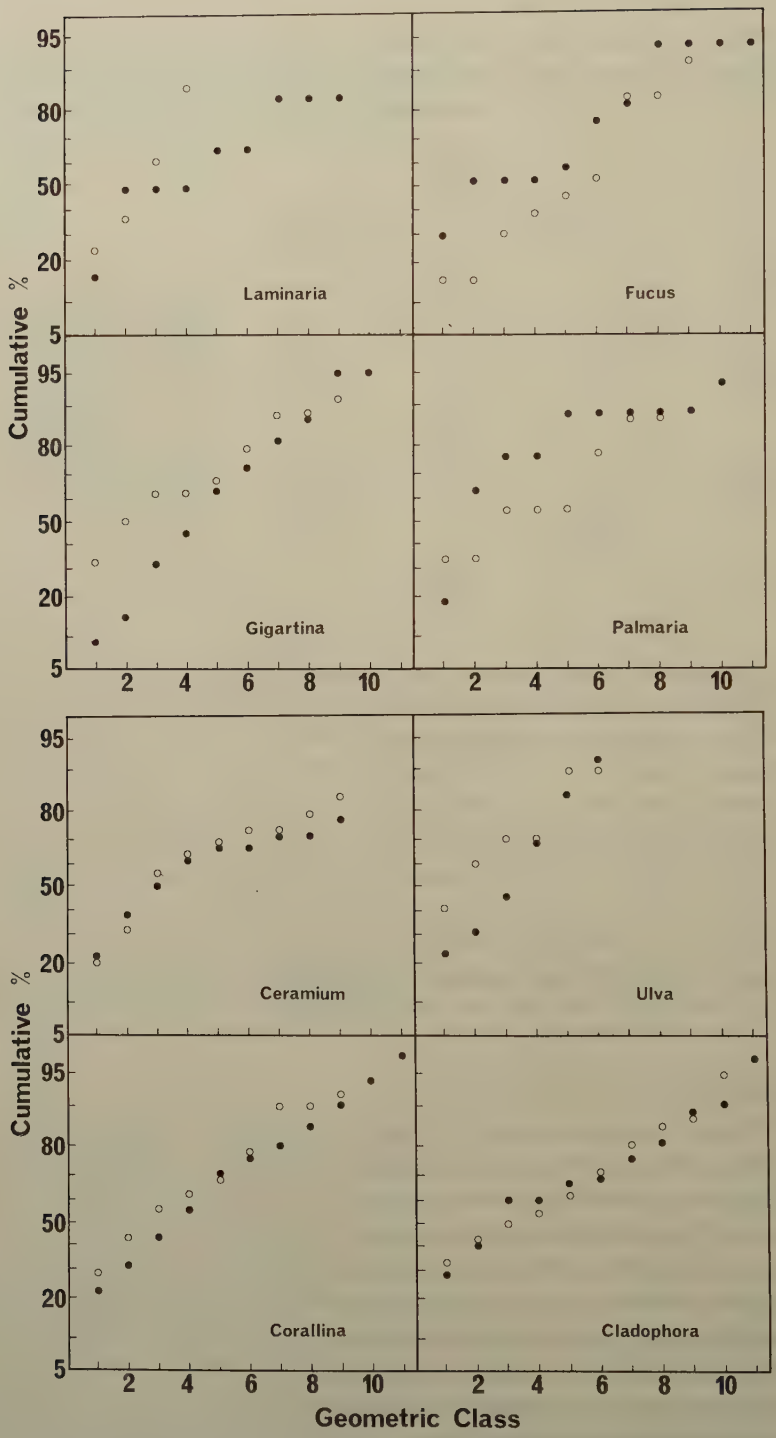

Fig. 3. Log-normal plots (see text for derivation) of harpacticoid species-abundance data from eight species of algae at St. Abbs (●) and Robin Hood's Bay (○): fitted lines are intentionally omitted for clarity.

tures from a straight line are considered as points of unconformity and thus represent communities out of equilibrium.

Log-normal plots are shown in Fig. 3 for the eight species of algae at both sites. These data indicate that whilst some copepod assemblages conform to a theoretical log-normal model, others clearly do not. The best fits are with *Corallina*, *Cladophora*, and *Ulva* which may be regarded as having approximated to a state of species equilibrium. Of more immediate interest, however, are substrata which show either more conformity at one site than at the other (*Laminaria*, *Palmaria*, *Fucus*, and *Gigartina*), or show non-conformity at both sites (*Ceramium*). At Robin Hood's Bay, *Laminaria*, *Fucus*, and *Palmaria* showed fewer deviations from a straight line than did the same algae at St. Abbs, while *Gigartina* deviates more at Robin Hood's Bay than at St. Abbs. Dominance influences the slope of the line and goodness of fit. At Robin Hood's Bay these algae have fewer geometric classes spanned than at St. Abbs representing higher evenness of individuals amongst species (see also Table IX). An extension over additional geometric classes at St. Abbs results from a large increase in abundance of some species; shallow log-normal plots extending over many geometric classes represent an overall greater dominance, characteristic of disturbed conditions. To illustrate this point, consider *Laminaria*. At St. Abbs its fauna was greatly dominated by *Harpacticus chelifer* which draws abundance classes to the right and reduces the slope of the plot. At Robin Hood's Bay, *H. chelifer* was of minor importance, being represented by only one individual on this alga. The steepness of the plot at Robin Hood's Bay, in the absence of such a highly dominant species, suggests that the niche occupied by *H. chelifer* at St. Abbs remains unexploited at Robin Hood's Bay.

At both sites, *Ceramium* showed a typical non-equilibrium plot (sensu Gray & Mirza, 1979) characteristic of short-lived or disturbed environments (Fig. 3). This is consistent with information already presented regarding species associations and interactions. Immigration of species from immediately surrounding habitats rapidly increases the species pool throughout the season (Fig. 4), but fluctuations are great as species come and go. As these colonizing species increase in abundance on *Ceramium*, the rates at which resources are utilized will increase until they become limited by the rates at which they are provided. Resource specialization will be the ultimate outcome of these events leading to higher species packing (e.g. May & MacArthur, 1972), and a balance between incoming and outgoing species. Before such an equilibrium state is realized, however, the substratum becomes precarious due to seasonal diminution of the *Ceramium* population. A colonization curve fails to reach an asymptote through the points in Fig. 4 and emphasizes that within the life cycles of those harpacticoid species involved, an equilibrium community does not establish in such ephemeral habitats. Community structures of this kind are typically induced by physical or biological perturbations of low predictability (Sanders, 1979). For if the habitat is persistent there develops a dynamic equilibrium of species immigration and extinction (e.g. *Corallina*). On temporally unstable algae, however, (apart from

Ceramium) which attain their maximum abundance over the spring and summer months and which are later dislodged in large quantities by autumnal gales, apparent equilibrium assemblages can also develop (e.g. *Ulva*). In this instance the specific properties of the substratum and life cycle characteristics of component copepods seem to be important. *Ulva* is attractive as a habitat only to a small number of eurytopic species (see p. 167) which are indifferent to the presence of algal antibiotics; other species are apparently excluded. It is suspected that these invasive eurytopic species quickly attain a state of equilibrium through rapid life cycle adaptations.

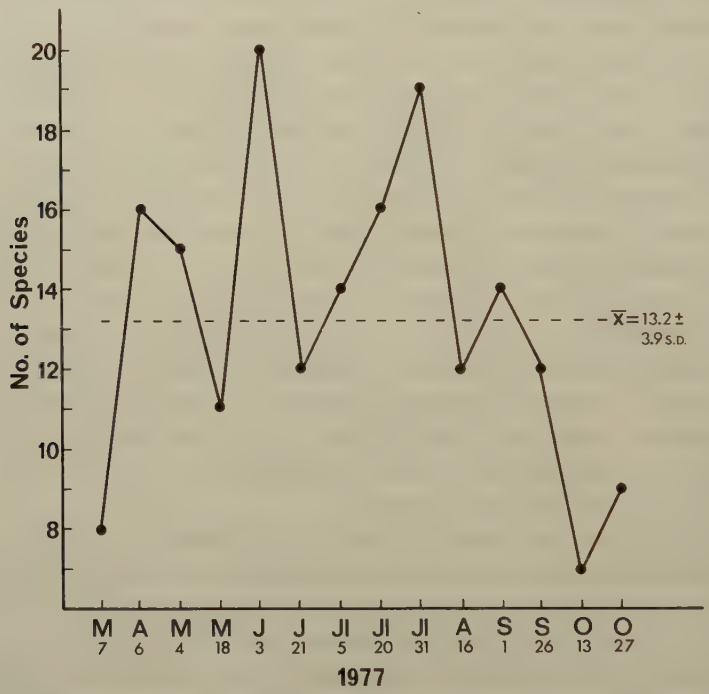

Fig. 4. Number of harpacticoid species sampled regularly from *Ceramium* at Robin Hood's Bay, March–October 1977: data collected as part of a separate study (Hicks, 1979).

Poor fits to the model have also often been related to low numerical and species abundances (see Warwick & Buchanan, 1970; Gage & Tett, 1973); in instances where lack of conformity occurs with more abundant species, non-representation of particular geometric classes is often responsible. For example, St. Abbs *Fucus* has classes 3 & 4 and 9 to 11 missing which produces a stepped line of poor fit. Why some geometric classes fail to be represented is not known. It could be by chance, or it may concern biotic factors such as recruitment failures etc. Significantly, those species associated with departures at geometric class 4 on *Ceramium* at St. Abbs are the tisbids *Tisbe furcata* and *Scutellidium longicauda*. *Tisbe furcata* was also consistently involved in deviations on Robin Hood's Bay *Palmaria* (class 3), *Ulva*

(class 5), and *Corallina* (class 7), while *T.* ? *minor* responded similarly on Robin Hood's Bay *Gigartina* (class 7) and St. Abbs *Cladophora* (class 3). Species within the genus *Tisbe* have been recognized as opportunists (e.g. Marcotte & Coull, 1974; Fava & Volkmann, 1975), and similar attributes pertain to *Scutellidium* which, in other situations, is often found in high numbers on decaying sublittoral drift algae (pers. obs.). In other algal assemblages e.g. *Palmaria* and *Laminaria* from St. Abbs, and *Fucus* and *Gigartina* at Robin Hood's Bay, another tisbid *Sacodiscus littoralis* is also associated with significant deviations at geometric classes 5, 7, 7 and 3, respectively. Clearly the specific life histories characteristic of tisbids are implicated; they are highly responsive to environmental disturbances. Conditions favouring the growth and population expansion of numerically dominant species may also be operating on these opportunistic species. The opportunists tend to increase in numbers faster than other associates, and in so doing shift into higher geometric classes; the outcome in terms of a log-normal pattern is to reduce conformity by producing a break point in the line.

TABLE XII

Relation of conformity to log-normal plot and surface area of algae at Robin Hood's Bay and St. Abbs: rankings are from poor conformity (1) to good conformity (8); N.S., not significant.

Algal species ranked by surface area	Surface area (cm^2)	Rank by conformity to log-normal	
		Robin Hood's Bay	St. Abbs
Laminaria	7	6	2
Fucus	12	4	4
Gigartina	38	3	5
Palmaria	43	2	1
Ceramium	80	1	3
Ulva	110	5	6
Corallina	120	7	8
Cladophora	216	8	7
		$r_s = 0.405$ N.S.	$r_s = 0.714$, $P = 0.05$

To examine the impact of habitat complexity on the goodness of fit to the log-normal, the plot of each alga from both sites was ranked (Spearman r_s) according to its apparent departure from a straight line. No significant correlation emerged between surface area and conformity of the data to the log-normal at Robin Hood's Bay ($r_s = 0.41$), but the correlation for the St. Abbs data was somewhat better ($r_s = 0.71$, $P = 0.05$, Table XII). Furthermore, linear regression of geometric class on probit transformed cumulative percentage showed highly significant correlations ($0.01 > P > 0.001$) for all algae at both sites, a result anticipated because of the consistent increase in slope derived from plotting cumulative percentages. Ranking the level of correlation coefficients against surface area confirmed the result of the

Spearman test with overall better fits to the log-normal at St. Abbs than at Robin Hood's Bay. These results are also consistent with the findings on species diversity.

Discussion

This enquiry has focussed on one of the primary features regarded as affecting species diversity, namely spatial heterogeneity or habitat complexity (Monge & Sutherland, 1976). By investigating a gradient of complexities represented by different species of marine algae from essentially the same tidal level, it has been possible to corroborate in part the prediction advanced for terrestrial communities, that increases in micro-spatial complexity allow for linearly related increases in diversity (e.g. MacArthur & MacArthur, 1961; Pianka, 1967; Karr & Roth, 1971).

That habitable space and trophic resources are directly implicated in the derivation of diversity–complexity relations is substantiated by an interpretation of inter-site environmental differences. Site characteristics in the sense of exposure, algal distribution, and harpacticoid species composition and richness are in general comparable, but algae at St. Abbs supported over twice the number of individuals than at Robin Hood's Bay. Moreover, species richness and faunal diversity showed significant concordance with algal complexity at St. Abbs while at Robin Hood's Bay there was a discordant relation (Table X). Site comparability departs markedly, however, when consideration is given to water turbidity and silt deposition (Moore, 1972, 1973a). St. Abbs is a clear water environment and the consistent diversity and species–area relation argues strongly for acceptance of the hypothesis that diversity of the permanently submerged algal fauna is well predicted if not largely determined by the structural complexity of individual species of algae. Gorman & Karr (1978) showed how departures from significant linearity in diversity–complexity investigations can be due to the influence of many natural or man-induced disturbances. Contrasting with St. Abbs, Robin Hood's Bay represents a turbid site, and in the present context turbidity is regarded as a sufficiently powerful environmental factor to cause deviations from linearity expected from the predictive model and portrayed in the clear water site of St. Abbs.

At Robin Hood's Bay, fine inorganic particulate matter settles out predominantly in summer, leaving a dense coating on algal surfaces. Moreover, divaricated algae have a greater propensity for trapping and retaining silt (Table I) and frond axils become packed with fine material often bound with muco-substances derived from both the alga and associated organisms. This, while not altering the fundamental habitable surface, appreciably reduces the realized surface. Unlike accumulations of coarser debris which can actively promote habitat heterogeneity (Hicks, 1977a, b), the reduced pore space and greater load of fine particles eliminates a potentially important niche resource. Smoothing out of structural irregularities in this way and the infilling of habitable space reduces the potential carrying capacity of the habitat.

Apart from clogging of micro-habitat spaces, small diameter particles may interfere with feeding processes and ingestive behaviour and may also assist in lowering absolute food availability by reducing primary production of epiphytic autotrophs. Fraga (1976) reported an estimated 36% reduction in primary productivity attributable to light attenuation by suspended inorganic matter (clay). On the other hand, because of their proportionally larger surface area, small diameter particles may support higher population levels of heterotrophic bacteria (ZoBell, 1946). But, while this may produce more bacterial food at Robin Hood's Bay, the corresponding reduction in space and autotrophic activity may have a counterbalancing effect, which while not necessarily leading to species exclusion could limit population expansion. These may be the principal features responsible for the lower overall abundance of copepods at Robin Hood's Bay. The effect of total number of individuals has been shown to be of minor importance in the calculation of an index of diversity, but higher diversities on structurally simple algae such as *Fucus*, *Gigartina*, and *Laminaria* relative to a complexity gradient are sufficient to eliminate the positive linearity predicted and confirmed in the St. Abbs data. Thus, the large residual variance obtained from regression analyses on community parameters at Robin Hood's Bay (Table X) is suggested to be the result of long-term contamination of algae by clay, acting as an exogenous dampening factor, modifying the outcome of community structuring phenomena manifested at a clear water site.

Mechanisms whereby complex habitats are capable of greater species packing (May & MacArthur, 1972) are predominantly based on the behaviour patterns of individual species. Certain algae have distinctive growth forms and other niche requirements which meet the specific needs of various species. Major differences between algae may be the occurrence of structural elements in the vegetation, critical in determining species composition. Features such as fine cylindrical fronds, bryozoan zooecia etc. have already been suggested as influencing the occurrence of such groups as the laophontoids. Some species are highly responsive to particular formations and also to particular micro-states within these formations.

Coexisting harpacticoids often forage at different spatial levels within an algal habitat (see also Ott, 1967, for nematodes), thereby effectively partitioning food resources and assisting in lowering competitive interactions. In the densely populated assemblage associated with *Corallina* in New Zealand (Hicks, 1977b), in situ observations indicated how some species confined themselves to the sandy sediments at the base of the alga, while others were vertically stratified and were located predominantly on the erect fronds. Divergent stratal preferences (or restrictions) must undoubtedly have influenced the species selection of different algae and of microhabitats within each substratum. Such demonstrations of microhabitat subdivision are comparable to the well-known vertical stratification in vegetation of terrestrial organisms (e.g. Cody, 1968; Edington & Edington, 1972; Schoener, 1974). It can also be argued that in dense assemblages differences in body size such as those noted for *Harpacticus obscurus* on St. Abbs *Ceramium* may be important in resource

partitioning. In many harpacticoids size differences between species are minimal. Within most species, however, sexual selection has apparently favoured sexual dimorphism in body size (with females usually being larger than males), and consequently size differences in feeding apparatus. Sexes may diverge in food choice and this, apart from reducing intraspecific competition, may allow them to utilize food supplies more efficiently. But, in guilds where no detectable differences in size or morphology are apparent, behavioural means of ecological segregation may again be critical. Ivester & Coull (1977) recently investigated two sympatric species of *Enhydrosoma* and were unable to provide evidence of a structural difference regarded as sufficient to allow competitive avoidance (although they did not examine in detail the cutting edge of the mandibles). In this case behavioural variability was considered to be at a level sufficient to allow coëxistence.

With any increase in substratum surface area comes a potentially increased supply of sessile food and, in theory, a greater opportunity for a higher diversity in food organisms. As reflected in the fauna, this is a natural response to greater relative habitable space. While not considering bacteria, known to be important dietary components to harpacticoids (Rieper, 1978), Fretter & Manly (1977) counted the number of species and abundance of epiphytic diatoms on a range of algae, including some of those at present being studied. Significantly, they concluded that *Cladophora* supported larger numbers of cells than other, less complex, algae such as *Fucus* and *Palmaria*. These latter two species not only showed lower densities of diatoms but also lower generic richness. The function of a large surface area in providing increased settlement space is contributory to the higher values in *Cladophora*. Paradoxically, one of the algae with the lowest densities of diatoms was *Corallina*, which because of the abundance and diversity of harpacticoids it is known to support may have been expected to show a higher diatom diversity. As outlined previously, however, high diversity of harpacticoids on *Corallina* is attributed not only to those living and feeding off frond flora, but also to those associating with deposited detritus and sediments. Because of its erect growth form *Corallina* acts as a more effective accumulator of both suspended inorganic and organic particles. Accordingly levels of deposited material are higher than for other algae (Fretter & Manly, 1977; Hicks, 1977a). These materials act as a substratum for considerable diatom and bacterial populations (pers. obs.) capable of maintaining a diverse assemblage of harpacticoid browsers.

For reasons outlined elsewhere (Hicks, 1979) nutritional resources are considered to be more temporally uniform on phytal than on terrigenous substrata. Diverse unlimited food reserves on surfaces of high complexity will allow for increased trophic specialization and tighter species packing. The present results are testimony to this opinion.

Apart from offering greater habitable space and more diverse nutritional resources, physically or biogenically complex environments also permit a moderation or protection from predation by the provision of spatial refuges (Menge &

Sutherland, 1976; Heck & Wetstone, 1977; Woodin, 1978). Predators on harpacticoids in other biotopes include caprellid amphipods (Caine, 1978), polychaetes (Fauchald & Jumars, 1979; Shaffer, 1979), decapods (Wicksten, 1977), and fish (e.g. Sibert, 1979) as well as other members of the meiobenthos, e.g. turbellarians, nematodes, and cnidarians (Smol & Heip, 1974; Spoon & Blanquet, 1978). Predators of phytal harpacticoids have not been adequately defined, yet a few authors have reported predation by small "picker-type" fishes (e.g. Bray & Ebeling, 1975; Zander & Heymer, 1977). These latter authors ascribe up to 66% of the diet of littoral blennioid and gobiid fishes to phytal harpacticoids. Roland (1978) provided evidence of a four-step food chain in a *Macrocystis* frond community where harpacticoids feeding on epiphytic diatoms were preyed upon by clingfish which in turn succumbed to predation by larger fish. Most of these reports are not from structurally complex algal systems, so it is difficult to evaluate either how effective a refuge finely branched algae like *Cladophora* and *Corallina* might be, or what the relative impact of predation might be in simple versus structurally diverse algal assemblages. Nevertheless, one might justifiably predict that predation of harpacticoids inhabiting complex algae is potentially reduced because of impenetrability by large predators into refuge centres.

On the basis of reproductive and life-history characteristics, Hicks (1979) proposed that marine algae represented unpredictable substrata to resident harpacticoids. This conclusion is endorsed in the present analysis by the incidence of poor fits to the log-normal, a model capable of detecting community disequilibrium (Gray, 1978; Gray & Mirza, 1979). The probability of algae being torn away by water turbulence or destroyed by larger herbivores or decomposition processes, leads to temporal habitat flux. Temporal persistence of substrata assists in the development of equilibrium communities and of the algae here represented, *Corallina* and *Cladophora* come closest to this state. As already indicated, however, if the particular harpacticoid species concerned are capable of rapid adaptation and population regulation, even short-lived substrata can develop equilibrium assemblages (e.g. *Ulva*). Other short-lived algae sustaining species with more protracted life-cycle requirements do not attain equilibrium states; temporal instability leads to an undersaturation of species causing greater oscillations in the rate of immigration and emigration (e.g. *Ceramium*, see Fig. 4). If in this instance species interactions (e.g. competition) became an important factor affecting community structure we could expect species packing to be more even than random (Sale, 1974). Species associated with ephemeral substrata may be regarded as typical opportunists which phase in and out over very short time sequences as a result of high reproductive and generation turnover.

The influence of habitat complexity and turbidity on assemblage equilibrium remains to be considered. If we accept that a more complex habitat will accumulate a larger number of species than a less complex habitat, and since species extinction rate is predicted to vary inversely to complexity (≡area, MacArthur & Wilson, 1967), the net outcome of a more complex habitat should be a higher number of

species involved in reaching equilibrium. A significant correlation of surface area to a log-normal distribution at St. Abbs (Table XII), supports this view and implies that as complexity of the environment increases the availability of a greater number of niches allows for greater species packing and a greater spread of individuals over several geometric (abundance) classes. The influence of turbid conditions at Robin Hood's Bay reduces potential niche space and leads not only to less conformity to the log-normal distribution (Table XII), but also to less clear-cut diversity–surface area relations (Table X).

The better relation of species diversity and log-normal conformity to complexity at St. Abbs suggests that clear water assemblages are in a greater relative state of equilibrium than those influenced by turbidity. This endorses Gorman & Karr's (1978) remark that the more the community reflects a non-equilibrium state the greater will be the deviation from a linear association between diversity and habitat complexity.

The present study has demonstrated the importance of biologically generated substratum complexity in the regulation of diversity patterns. Similarly, Thistle (1978, 1979) attributed high deep-sea harpacticoid diversity to delicate biogenic structures such as agglutinated foraminiferan tests and polychaete mudballs, features either overlooked or disregarded by earlier workers when sieving and washing benthic samples. That environmental stability (sensu Sanders, 1968) is required to permit these structures to remain intact is clear, but their mere presence greatly increases structural complexity at the sediment surface allowing greater differential space exploitation. The interplay between apparent proximate and ultimate causal factors may at first seem confusing, but emphasizes how one diversity hypothesis need not be mutually exclusive of others (Huston, 1979; Thistle, 1979). After all, the highest harpacticoid diversities yet recorded from the marine environment (Table XI) are those from a disturbed (turbulence induced) shallow-water kelp holdfast habitat (Moore, 1973b), which because of its complex structure is capable of supporting a diverse array of species both at the level of the taxocene and of the whole community.

Acknowledgements

This investigation was undertaken during tenure of the Garstang Research Fellowship from the University of Leeds. I thank Dr. J. R. Lewis for the provision of research facilities at the Wellcome Marine Laboratory, and for his enthusiastic discussions during my stay at Robin Hood's Bay. I appreciate the positive suggestions of Dr. P. G. Moore and Professor J. S. Gray whose critical evaluations of the manuscript have assisted greatly in its improvement. Finally, I recognize the helpful comments on various drafts of this paper by my colleagues at Robin Hood's Bay.

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ASPECTS OF FOOD INTAKE, FOOD SELECTION, AND ALIMENTARY CANAL MORPHOLOGY OF *MUGIL CEPHALUS* (Linnaeus, 1958), *LIZA TRICUSPIDENS* (Smith, 1935), *L. RICHARDSONI* (Smith, 1846), AND *L. DUMERILI* (Steindachner, 1869)

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Abstract: Feeding periodicity, selection efficiency and food consumption of *Liza dumerili* (Steindachner, 1869) and *L. richardsoni* (Smith, 1846) were determined. The effects of particle size and nature of ingested food on aspects of the morphology of the alimentary canal of *L. dumerili*, *L. richardsoni*, *Mugil cephalus* (Linnaeus, 1958) and *Liza tricuspidens* (Smith, 1935) are discussed. It was found that the dominant mullet species in the Swartkops estuary (South Africa) not only exhibit different feeding periodicities (*L. dumerili* and *L. richardsoni*) but that selected material in all the species differs in chemical as well as physical properties. Alimentary canals of each species are morphologically well adapted for selection, ingestion and digestion of its preferred food items. These factors reduce interspecific competition among the different mullet species.

Introduction

The natural diet of a number of mullet species from estuaries and the coast of South Africa has been fairly well established. Allowing for interspecific differences, food of larger fish consists mainly of sediment particles, decaying plant detritus and micro-algae, including epiphytic and benthic forms (Gilchrist, 1918; Smith, 1935; Day, 1951; Scott *et al.*, 1952; Day & Morgans, 1956; Macnae, 1957; Masson & Marais, 1975; Blaber, 1976). The general nature of the food of mullet has been summarized by Thomson (1954) "although some differences have been found in the amount of the larger microscopic animal matter ingested, in general, mullet ingested whatever organic food of suitable size was common in the area in which they were feeding".

Since the natural diet (Masson & Marais, 1975) and chemical composition of alimentary canal contents (Marais & Erasmus, 1977) of mullets in the Swartkops estuary have been documented, feeding periodicity and selection efficiency of *Liza dumerili* (Steindachner, 1869) and *L. richardsoni* (Smith, 1846) will be discussed. Odum (1970) suggested that mullet populations adjust morphologically to the type of food available in the environment by lengthening the intestine for coarser diets. The effect of particle size and nature of ingested food on aspects of the morphology

of the alimentary canal of *L. dumerili*, *L. richardsoni*, *Mugil cephalus* (Linnaeus, 1958), and *Liza tricuspidens* (Smith, 1935) will also be considered.

METHODS

GENERAL

Seine netting was performed at four locations in the Swartkops estuary that differed in substratum properties (Fig. 1). Station 1 was near the mouth where *Zostera capensis* Setchell occurred on submerged firm muddy areas. Marginal vegetation consisted of *Spartina capensis* Nees ex Trin. extending into the *Arthrocnemum* sp. The substratum of Station 2, at the mouth of a creek, was soft, rich and silty. In contrast to Station 2, Station 3 consisted of an open coarse sandy beach which could be covered by a thin layer of yellow silt after a flood. Station 4 consisted of two unstable pools at the head of the estuary. The substratum contained many pebbles and stones while the macrophytes *Cyperus textilis* Thunb. and *Pragmites australis* (Cav.) Trin. ex Steud. extended into the pools along the banks.

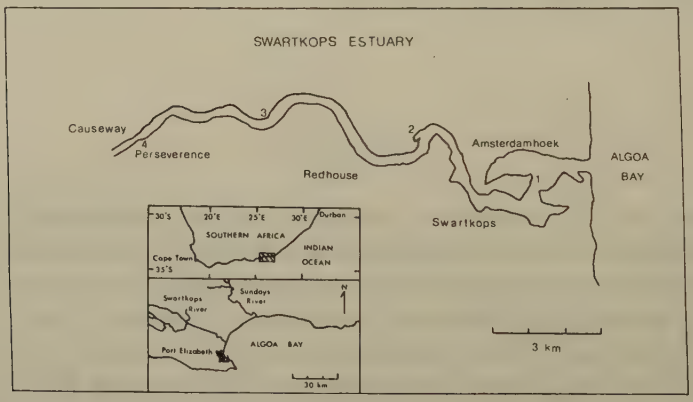

Fig. 1. Geographical position of Swartkops estuary and position of sampling sites.

FEEDING PERIODICITY

Two efforts were made at Station 1 (the only area suitable for this type of study) to determine feeding periodicity in *Liza dumerili* and *L. richardsoni*. The first (high tide during sunset and sunrise) was during June 1975 when seine netting was performed hourly. In the second operation (high tide during midday and midnight) during November 1978, netting was conducted 2-hourly. In the first study, specimens were deep frozen for subsequent length measurements and for weighing

stomach and intestine contents. For the second study fish were measured and alimentary canals removed and stored in 10% formalin. Stomach (also oesophagus contents in *L. dumerili*), intestine and rectum contents were removed and weighed at a later stage.

PARTICLE SIZE SELECTION

Fish were caught at all four stations. Stomach contents (also oesophagus in *L. dumerili*) were removed for wet sieving by the method described by Morgans (1956). The same procedure was followed for substratum samples collected at the same area (top 0.5-cm layer) where netting was performed. Endecotts sieves used for this purpose had mesh sizes corresponding to the Wentworth scale. Cumulative curves, to demonstrate the selective ability of different mullet species divided into different size ranges, were drawn for stomach contents and substratum particle composition from samples taken at Station 1. The median particle diameter, or the value on the *X*-axis corresponding to the 50% value on the *Y*-axis, is given in mm on the cumulative curves and in Table II for samples taken at Stations 2–4.

SELECTION FOR BIOCHEMICAL COMPONENTS

Chemical analysis to determine the crude fat (Goldfish apparatus), crude protein (nitrogen by micro Kjeldal method $\times 6.25$), ash (5 h at 450 °C) and carbohydrate (100 − ash + protein + fat) were performed on duplicate samples of the alimentary canal contents and substratum samples. Energy was calculated from the mean Joule values for fats (39 349), proteins (22 186), and carbohydrates (17 581) given by Schmidt-Nielsen (1975).

MORPHOLOGICAL CHARACTERISTICS OF THE ALIMENTARY CANAL

Standard length (SL), and intestinal length (IL) of a number of fresh mullets belonging to the four most abundant mullet species in the Swartkops estuary were measured to obtain a clearer understanding of the relationship between the ratio of IL to SL and food preference. Teeth development, relative size of the stomach and number and size of pyloric caecae were also related to the particular food preference of each species.

RESULTS

FEEDING PERIODICITY

Feeding periodicity of *L. dumerili* is graphically presented in Figs 2 and 3. From the graphs, it is clear that *L. dumerili* fed during the day and night but had a lower food intake during the night. Food intake was also less at low tide (Figs 2 and 3),

TABLE I

Mean body weight, standard deviation and size range of *Liza dumerili* and *L. richardsoni* caught during two 24-h studies for determination of feeding periodicity.

	L. dumerili			*L. richardsoni*				*L. dumerili*			*L. richardsoni*		
Date and time (h) 25 June 1975	Mean weight (g)	SD	Range (g)	Mean weight (g)	SD	Range (g)	Date and time (h) 10 Nov. 1978	Mean weight (g)	SD	Range (g)	Mean weight (g)	SD	Range (g)
1500	68.4	±27.1	27–120	40,6	±20,9	21–81	1400	88.7	±16.3	63–127	52,3	± 27.2	17–45
1600	65.1	±34.9	30–144	62,7	±15,4	37–74							
1700	43.7	±25.7	18–111	38,6	±17,6	23–80	1600	102.7	±19.9	71–135	32,3	± 11.2	17–45
1800	56.7	±30.3	16–112	48,2	±13,9	29–60							
1900	50.6	±10.6	38–74	34,0	–	–	1800	127.5	±45.7	60–230	60,0	–	–
2000	97.6	±29.9	58–156	–	–	–							
2100	68.6	±30.8	33–146	48,9	±14,3	33–74	2000	–	–	–	67,0	± 7,1	62–72
2200	57.0	±22.9	23–91	29,4	–	–							
2400	–	–	–	–	–	–	2200	109.2	±30.3	71–165	67,4	± 31,2	45–127
0100	–	–	–	–	–	–							
0200	–	–	–	–	–	–	2400	107.1	±34.4	70–182	42,5	± 0,7	42–43
0300	73,2	±36.3	16–138	64,3	±12,1	54–81							
0400	59,6	±13.0	45–70	62,1	±23,7	36–107	0200	125.0	±18.3	105–140	36,5	± 23,3	20–53
0500	–	–	–	80,1	±39,2	36–171							
0600	27,7	±23.8	11–63	52,4	±15,2	27–72	0400	96.3	±21.9	65–140	20,3	± 7,2	11–26
0700	155,1	–	–	72,9	±45,4	25–163							
0800	–	–	–	171,1	±96,5	62–290	0600	97.9	±37.2	63–171	183,0	± 43,8	152–214
0900	123,8	±57.1	23–185	41,1	±14,3	30–57							
1000	46,0	±20.3	28–80	31,6	± 5,6	19–37	0800	86.6	± 8.0	74–106	72,3	± 51,7	33–131
1100	86,3	±22.3	49–110	28,4	± 4,5	22–34							
1200	98,7	±29.8	74–177	32,4	± 5,6	22–44	1000	110.8	±41.3	61–188	190,2	±141,5	59–387
1300	64,3	±14.5	37–88	30,4	± 6,3	23–41							
1400	81,2	±19.9	53–123	33,7	± 7,7	24–51	1200	89.3	±35.7	60–195	50,8	± 23,3	30–107
1500	68,3	±30.3	19–111	33,3	±10,3	22–41							

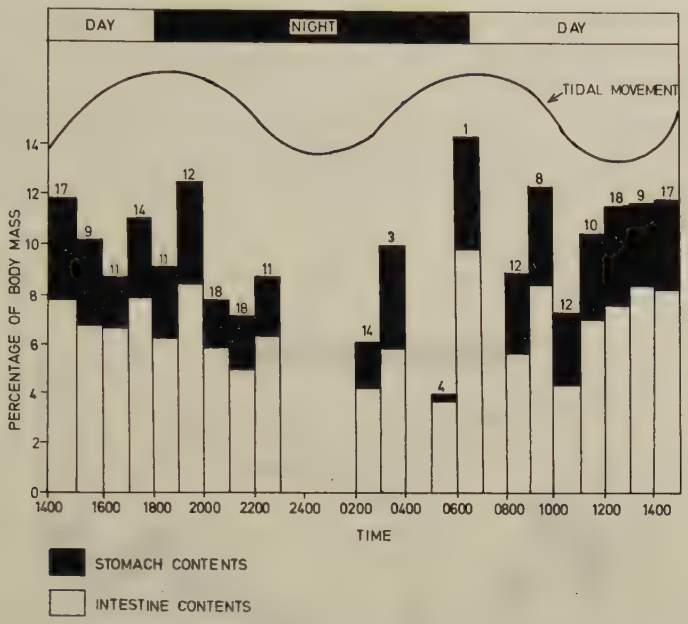

Fig. 2. Stomach and intestinal tract contents of *Liza dumerili* as a percentage of total body mass in relation to time of day and tidal movement.

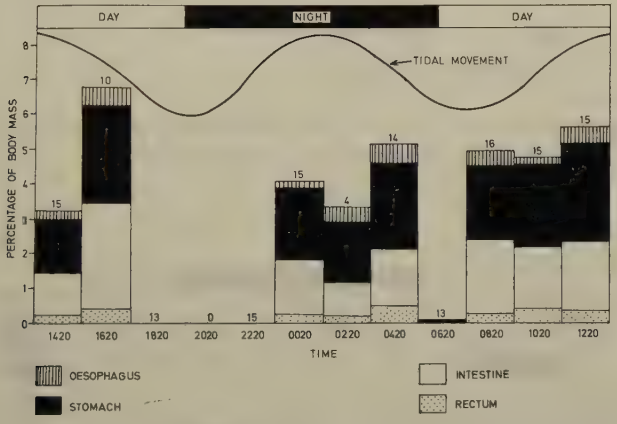

Fig. 3. Oesophagus, stomach, intestine and rectum contents of *Liza dumerili* as a percentage of total body mass in relation to time of day and tidal movement.

especially when low tide was during or close to hours of darkness. Less fish than normal were then caught and those caught had empty alimentary canals after being full only 2 h previously (sunset, Fig. 3). Body weights of *L. dumerili* that were analysed are given in Table I.

Figs. 4 and 5 graphically present food intake of *L. richardsoni* over a 24-h period. Three differences are evident when feeding periodicity of *L. richardsoni* is compared to *L. dumerili* (Figs. 2, 3, 4 and 5). The first is that *L. richardsoni* consumes considerably less food material than *L. dumerili*. Secondly this species has a much lower food intake during the night than *L. dumerili* and thirdly it seems to follow tidal movement closer than *L. dumerili*. Body weights of *L. richardsoni* that were analysed are given in Table I.

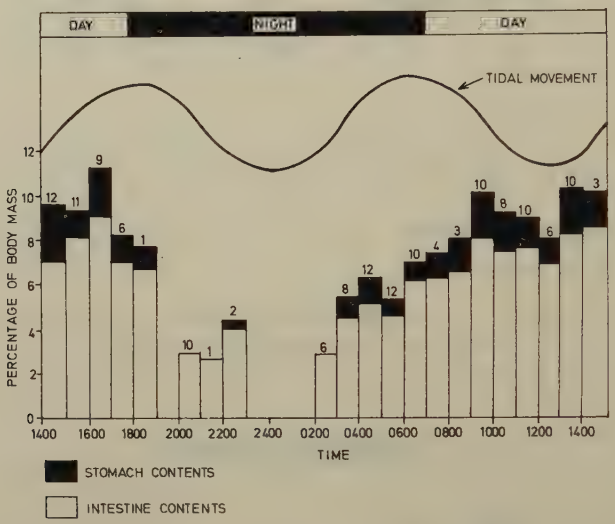

Fig. 4. Stomach and intestinal tract contents of *Liza richardsoni* as a percentage of total body mass in relation to time of day and tidal movement.

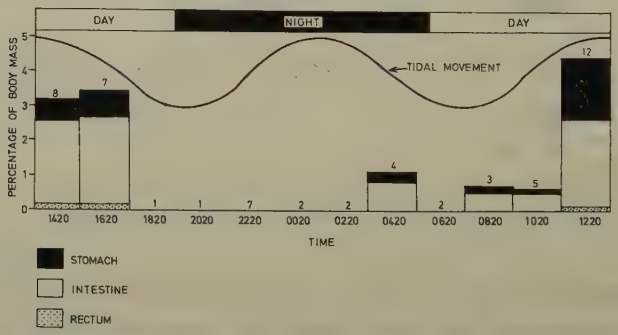

Fig. 5. Stomach, intestine and rectum contents of *Liza richardsoni* as a percentage of total body mass in relation to time of day and tidal movement.

PARTICLE SIZE SELECTION

Cumulative curves, to compare mean particle size of different mullet stomach contents with that of sediment fed on at Station 1 are given in Fig. 6. Comparisons for Stations 2–4 are given in Table II. Unfortunately different species were caught at different localities depending on the availability of the natural diet of each species in a particular environment. It is evident from Fig. 6 that *L. tricuspidens* ingested coarser material than either *L. dumerili* or *L. richardsoni*. *L. richardsoni*, on the other hand ingested finer material than *L. dumerili* caught in the same area.

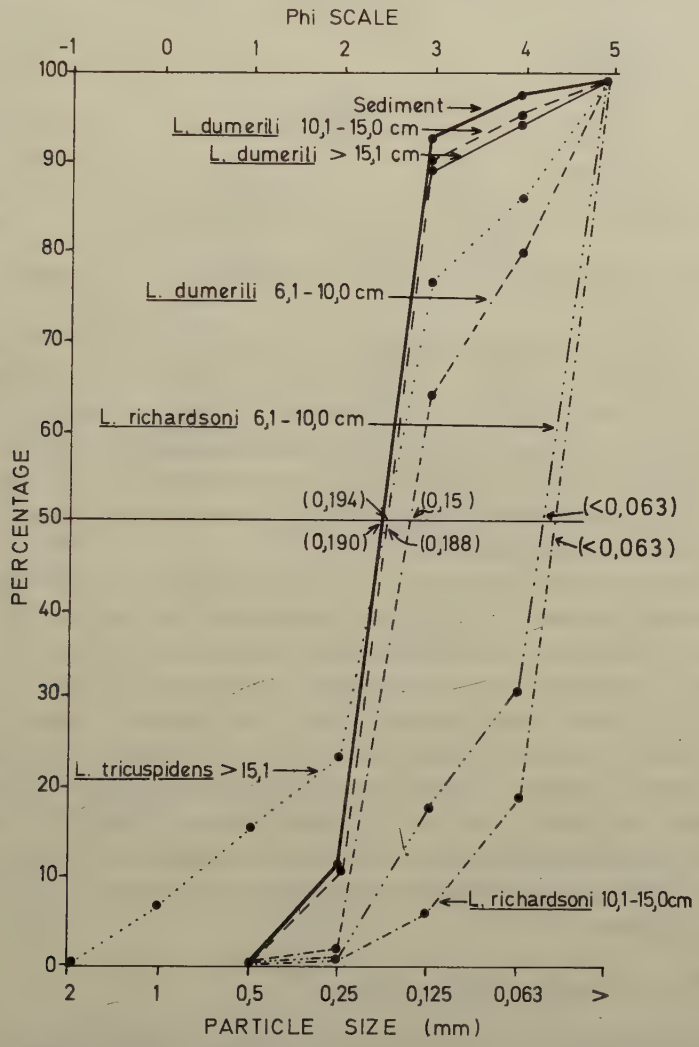

Fig. 6. Station 1: cumulative curves to compare mean particle size of *Liza dumerili* and *L. richardsoni* stomach contents with that of sediment on which fed (curve of *L. tricuspidens* stomach contents also included, although caught at the Amsterdamhoek side of Station 1).

TABLE II

The median particle diameter of substratum and stomach contents of *Liza dumerili* and *L. richardsoni* caught at Stations 2–4.

Station	Species	Size range (SL in cm)	Median particle diameter (mm)
2	*L. dumerili*	6.1–10.0	0.069
	L. dumerili	10.1–15.0	0.108
	L. dumerili	>15.1	0.124
	Substratum	–	61% < 0.063[a]
3	*L. dumerili*	6.1–10.0	0.188
	L. dumerili	10.1–15.0	0.244
	L. dumerili	>15.1	0.262
	Substratum	–	0.375
4	*L. dumerili*	6.1–10.0	0.190
	L. dumerili	10.1–15.0	0.174
	M. cephalus	6.1–10.0	59% < 0.063[a]
	Substratum	–	0.360

[a] Too much silt and clay in sample to determine median particle diameter.

Information on temperature, salinity, SL and number of fish used are given in Table III.

There was little difference in particle size ingested by *L. dumerili* in the size ranges 10–15 cm and >15 cm. *L. dumerili* of 6–10 cm, however, ingested smaller particles than either of the larger size ranges (Fig. 6). *L. richardsoni* in the size ranges 6–10 and 10–15 cm ingested fairly similar size particles (Fig. 6). This could be because the difference in SL between *L. richardsoni* of 6–10 cm and 10–15 cm (11.1 − 8.5 = 2.6 cm) was smaller than between *L. dumerili* of 6–10 cm and 10–15 cm (13.0 − 8.7 = 4.3 cm) (see Table III).

At the silty Station 2, where only *L. dumerili* was caught, all size ranges ingested coarser particles than was typical of the substratum from this locality (Table II). Smaller fish ingested finer material than larger fish. At the very coarse sandy Station 3, *L. dumerili* ingested finer material than was characteristic of the area (Table II) but it was still coarser than material taken in at Stations 1 and 2 (Fig. 6 and Table II). Smaller fish again ingested finer material. There was little difference in the mean SL of *L. dumerili* divided into two size ranges (6–10 = 9.2 cm; 10–15 = 10.8 cm) that were caught at the highly variable Station 4 (Table III). This probably explains the small difference in mean particle size ingested by the two size ranges (Table II). *Mugil cephalus* caught at this station ingested much finer material than *Liza dumerili* (Table II).

SELECTION FOR BIOCHEMICAL COMPONENTS

Selection efficiency of *L. dumerili* of two size ranges at two localities is presented in Table IV. Table IV shows that the selection efficiency of *L. dumerili* at a coarse sandy substratum was higher than at a fine silty substratum. The substratum at

TABLE III

Temperature and salinity values at collecting sites: mean SL and numbers of fish used for stomach particle size determinations only.

Station	Date	Temperature (°C)	Salinity (mOsm/l)	Species	Size range of fish					
					6.1–10.0 cm		10.1–15.0 cm		>15.0 cm	
					n	Mean SL (cm)	*n*	Mean SL (cm)	*n*	Mean SL (cm)
1 (a)	11 Apr. 1974	23.7	687	*L. dumerili*			13	12.5	6	15.7
1 (a)	1 Oct. 1974	19.0	1040	*L. dumerili*			27	13,1	44	17.1
1 (a)	13 Jan. 1975	23.0	1057	*L. dumerili*	13	8.7	20	13.0	14	16.3
				L. richardsoni	21	8.5	5	11.1		
1 (b)[1]	1 Mar. 1975	21.0	1066	*L. tricuspidens*					9	16.2
2	11 Apr. 1974	25.4	144	*L. dumerili*	11	8.6	10	12.2	4	16.0
2	2 Oct. 1974	23.5	5	*L. dumerili*	45	8.7	17	11.9		
3	10 Apr. 1974	24.0	80	*L. dumerili*	35	8.7	14	12.5	6	15.6
4	10 Apr. 1975	22.5	8	*L. dumerili*	3	9.2	7	10.8		
				M. cephalus	31	9.3				

[1] Amsterdamhoek side of Station I.

TABLE IV

Comparison of the selection efficiency of *Liza dumerili* of two size ranges (>15 cm and <15 cm SL) from two localities (fine silt, Station 2; coarse sand, Station 3).

	Fat (%)	Protein (%)	Carbohydrate (%)	Ash (%)	Energy (J/100 g)
Substratum Station 2 (fine)	0.172	0.693	2.096	97.039	58 992
L. dumerili > 15 cm	0.786	2.075	2.179	94.960	115 273
Substratum Station 3 (coarse)	0.053	0.282	0.424	99.241	15 796
L. dumerili > 15 cm (oesophagus)	0.223	1.002	1.255	97.520	53 069
L. dumerili < 15 cm (oesophagus)	0.752	1.330	1.402	96.516	83 746
Selection efficiency					
L. dumerili St. 2 > 15 cm	4.6 ×	3.0 ×	1.0 ×	–	2.0 ×
L. dumerili St. 3 > 15 cm	4.2 ×	3.6 ×	3.0 ×	–	3.4 ×
L. dumerili St. 3 < 15 cm	14.2 ×	4.7 ×	3.3 ×	–	5.3 ×

Station 2 was richer in biochemical components and energy, however, so that more nutritious substances were still ingested at that locality (Table IV). Smaller *L. dumerili* at Station 3 selected much more efficiently than larger fish. Selection efficiency for biochemical components by *L. dumerili* and *L. richardsoni* are compared in Table V. It is clear from this Table that *L. richardsoni* not only ingested finer material than *L. dumerili* (Fig. 6) but that this fine material was much more nutritious. Selection efficiency of *L. richardsoni* was about 100% better for most components than that of *L. dumerili*.

MORPHOLOGICAL CHARACTERISTICS OF THE ALIMENTARY CANAL

From Table VI, indicating IL: SL ratios (and numbers of caecae), it is clear that *Mugil cephalus* (4.47 : 1–4.65 : 1) had a ratio nearly twice that found in the other

TABLE V

Comparison of the selection efficiency of *Liza dumerili* and *L. richardsoni* caught at the same locality.

	Fat (%)	Protein (%)	Carbohydrate (%)	Ash (%)	Energy (J/100 g)
Substratum	0.139	0.338	0.505	99.018	21 846
L. dumerili					
Oesophageal contents	0.273	1.243	1.819	96.674	70 099
Stomach contents	0.174	0.668	1.184	97.974	42 483
L. richardsoni					
Stomach contents	0.606	1.406	4.068	93.902	126 875
Selection efficiency					
L. dumerili (oesophagus)	2 ×	3.7 ×	3.6 ×	–	3.2 ×
L. dumerili (stomach)	1.3 ×	2.0 ×	2.3 ×	–	1.9 ×
L. richardsoni (stomach)	4.4 ×	4.2 ×	8.1 ×	–	5.8 ×

TABLE VI

Relationship between the intestinal length (IL) and standard length (SL) of mullet of different size ranges: number of pyloric caecae and range included for each species.

	Mugil cephalus				*Liza dumerili*				*Liza richardsoni*				*Liza tricuspidens*			
Size range (cm)	IL : SL (±SD)	*n*	Mean SL (±SD)	Pyloric caecae (range)	IL : SL	*n*	Mean SL (±SD)	Pyloric caecae (range)	IL : SL	*n*	Mean SL (±SD)	Pyloric caecae (range)	IL : SL	*n*	Mean SL (±SD)	Pyloric caecae (range)
6.1–10.0	5.18 : 1 ±0.64	20	7.77 ±1.13	2 (2)	2.53 : 1 ±0.31	23	8.63 ±1.04	6 (4–7)	2.55 : 1 ±0.23	21	8.50 ±0.72	6 (5–7)				
10.1–15.0	4.65 : 1 ±0.47	5	13.44 ±1.74	2 (2)	2.45 : 1 ±0.12	20	13.02 ±1.22	6 (4–7)	2.65 : 1 ±0.10	8	10.86 ±0.67	6 (5–7)	2.45 : 1 ±0.32	11	13.08 ±0.96	6 (6 7)
>15.1	4.47 : 1 ±0.92	21	25.01 ±5.18	2 (2)	2.38 : 1 ±0.19	20	16.47 ±0.92	6 (4–7)	2.45 : 1 ±0.19	35	18.21 ±2.23	6 (5–7)	2.06 : 1 ±0.24	24	23.86 ±4.84	6 (6–7)

species. Of the remaining three species, which did not differ to any extent, *Liza richardsoni* (2.45 : 2-2.65 : 1) had a slightly larger ratio than the other species. The >15 cm size range of *L. tricuspidens* had the smallest ratio (Table VI). Of the four mullet species investigated, *Mugil cephalus*, with the longest intestine, had the smallest number (2) of pyloric caecae. These were also poorly developed compared to the other species. The other three species each had a mean of six caecae (Table VI). Fig. 7 gives diagrammatic sketches based on stereo-microscopic observation, of the dentition of the four mullet species. More pointed teeth were found in *Liza richardsoni* and *Mugil cephalus*, which have been shown to ingest finer material in the Swartkops than *Liza dumerili* and *L. tricuspidens*. *L. tricuspidens*, known to ingest filamentous algae and macroplant detritus (Masson & Marais, 1975) had relatively large sharp edged teeth.

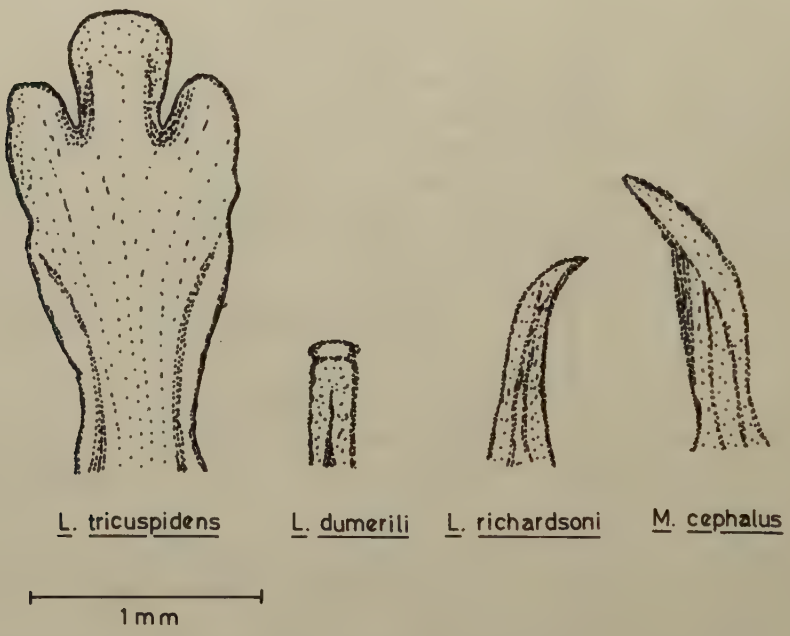

Fig. 7. Diagrammatic illustration of the teeth of *Liza tricuspidens*, *L. dumerili*, *L. richardsoni*, and *Mugil cephalus* of standard lengths 16.2, 15.6, 12.1 and 9.4 cm, respectively.

Discussion

There were marked differences in feeding periodicity between *L. dumerili* and *L. richardsoni* (Figs. 2–5), two species that are often caught together over a sandy substratum. Although both species consumed less food at night during the day, the differences were more pronounced in *L. richardsoni*. Food ingestion was also more

related to tidal movement in *L. richardsoni* than in *L. dumerili*. Both Thomson (1966) and Odum (1970) found a marked increase in rate of ingestion during rising and high tides in *Mugil cephalus*. Kuthalingham (1966), found no variation in feeding intensity for *M. cephalus* in relation to time of day. Blaber (1976) found that *Liza dumerili* and *Mugil cephalus* feed at reduced intensities during the night. *Liza macrolepis*, like *L. richardsoni*, apparently ceased to feed at night. Blaber (1976) concluded that the differences in peak feeding times of species occupying the same environment, might serve to reduce competition.

Digestion rates of *L. dumerili* and *L. richardsoni* can be approximated from the feeding periodicity data. Darnell & Meierotto (1962) cited work indicating that digestion rates of fish are influenced by factors such as type of food, amount of food, temperature, age and general activity of animals. Odum (1970) determined the retention time (dependent on digestion rate) of *Mugil cephalus* and found that it ranged from 2–6 h with a mean of between 4 and 5 h which means a turnover rate of five times in 24 h. From Fig. 4 it can be seen that retention time was shorter in *Liza richardsoni* and probably ranged between 3 and 4 h (1700–2100). Too few *L. richardsoni* were caught in November 1978 (Fig. 5) to confirm this estimate. The continuous feeding habit of *L. dumerili* made it more difficult to establish retention time accurately. Whereas none of the 12 fish caught at 2000 (Fig. 2) had an empty stomach, stomachs of 9 out of 18 specimens caught an hour later and 7 out of 18 caught 2 h later were empty. All 12 fish caught 2 h after 1620 during November 1978 and all 13 caught 2 h after 0420 had completely empty stomachs (Fig. 3). Retention time thus appears to be extremely short in *L. dumerili* and is probably between 1 and 2 h.

The maximum stomach contents, expressed as a percentage of body weight, amounted to ≈5% in *L. dumerili* (Figs. 2 and 3) and 3.5% in *L. richardsoni* (Figs. 4 and 5). Food consumption was determined according to Odum (1970), allowing for lower intake during the night. Assuming a turnover rate of 12 times for *L. dumerili* (2 h retention of food) a 100 g specimen would consume 60 g (12 × 5 g) wet material per day. A similar size *L. richardsoni* would consume 21 g (6 × 3.5 g) at a turnover rate of 6 times.

In the Swartkops estuary *L. dumerili* selected sand particles smaller than 0.5 mm (Fig. 6 and Table II). Even when the percentage of particles measuring 0.5 mm and more comprised 34.5% of the substratum at Station 3, all three size ranges of *L. dumerili* selected less than 3% of these size particles (Table II). Blaber (1976) found that *L. dumerili* from St. Lucia ingested particles with a mean size of 0.3 mm (range 0.25–0.40). It is also evident from Fig. 6 and Table II that the smaller size range (6–10 cm) of *L. dumerili* selected much finer material than the larger size ranges. This contrasts with the finding of Blaber (1976) who found that no change in diet and particle size preference occurred according to age in 10 mullet species from St Lucia. At Station 2, where silt and clay comprised 61% of the substratum, the smaller size range of *L. dumerili* contained 46% silt and clay in the stomach whereas it was only 20 and 31% respectively in the larger size ranges. It thus ap-

pears that although *L. dumerili* rejects particles coarser than 0.5 mm, even the smaller size range did not consume large amounts of exceptionally fine material when abundantly present. *L. richardsoni* of the same size range, consumed much finer material than *L. dumerili* of the same size range caught at the same locality (Fig. 6). This was also true for *Mugil cephalus* at Station 4. The median particle size for *M. cephalus* at this station was <0.063 mm and for *Liza dumerili* 0.174 mm (Table II). Blaber (1976) found that the mean particle size ingested by *Mugil cephalus* in St Lucia was 0.3 mm.

Marais & Erasmus (1977) reported that *M. cephalus* and *Liza richardsoni* alimentary canal contents contained much larger amounts of protein and carbohydrates than that of *L. dumerili*. The reason for this is the finer material ingested by these species (Fig. 6 and Table II). Odum (1968) and Wood (1964) found that *Mugil cephalus* prefers very fine particles and that these are richer in adsorbed organic material. The considerable amount of coarse material ingested by *Liza tricuspidens* (Md = 0.194 mm; Fig. 6) was due to large plant fragments typical of the natural diet of this species (Masson & Marais, 1975). The little sand ingested with the plant material by *L. tricuspidens*, was of a very fine nature (collected in a sieve with aperture 0.125 mm). The large amount of plant material was the main reason why food ingested by *L. tricuspidens* had a higher protein and carbohydrate content than that of the other species (Marais & Erasmus, 1977). The better selective ability of *L. richardsoni* as regards particle size (Fig. 6) and biochemical components (Table V) probably allowed this species to ingest less material and have a longer retention period and yet still obtain enough nutrition in the same environment as *L. dumerili*. The morphology of the alimentary canal of *L. richardsoni* is geared towards the handling of less material of higher quality than the other species.

According to Odum (1970) mullet populations adjust morphologically to the type of food in the environment by lengthening the intestines when ingesting coarser diets. This was also found for *Chanos chanos*, a fish with very similar feeding habits to mullets (Hiat, 1944; Schuster, 1949). Odum expressed the opinion that an intestine to fish length ratio of 3.2 : 1 (for *Mugil cephalus*) is adequate to assimilate a diatom diet, while a longer intestine is needed to extract nourishment from plant detritus and blue green algae. Hickling (1970) also suggested that the longer gut of larger grey mullet may be an adaption to food which contains a higher proportion of indigestible matter. From the IL : SL ratios of more than 4.5 : 1 (Table VI) it seems that *M. cephalus* is adapted to a fairly coarse algal diet in the Swartkops estuary. Considering the coarse macroplant and algal diet typical of *Liza tricuspidens* the IL : SL ratio (Table VI) appears unexpectedly low, but the presence of undigested algal filaments longer than 20 cm in the intestines may explain the apparent contradiction (Marais, 1976). This suggests that diatoms and bacteria attached to the plants and algae are probably of greater nutritional significance than the plants themselves. Whether this is so, is unknown, but it has been reported for *Tilapia esculenta* from Lake Victoria (Fish, 1951) and *Rhabdosargus holubi* from the West

Kleinemond estuary (Blaber, 1973). Low ratios of IL : SL found for *Liza dumerili* and *L. richardsoni* (Table VI) are in accordance with Odum's theory, judging from the abundance of diatoms ingested by these species (Masson & Marais, 1975). From visual observation *L. dumerili* had the largest stomach in relation to body size of the species studied. A large stomach and short but wide intestine could be advantageous to a species ingesting large amounts of sand together with relatively small quantities of very nutritious micro-algae. The same argument holds for *L. tricuspidens* which probably uses plant material instead of sand as a carrier medium. Smallest stomachs were observed in *Mugil cephalus* and *Liza richardsoni* which ingested the finest material. In contrast to *L. richardsoni*, however, *Mugil cephalus* is equipped with a very long intestinal tract which enables it to effectively digest a more fibrous diet.

Although Thomson (1954) could not explain the significance of the number of pyloric caecae, Babak (1903) and Kawai & Ikeda (1971) are of the opinion that the caecae assist in digestion of food material. Of the four species obtained from the Swartkops, *M. cephalus*, with the longest intestine, had the smallest number (2) and least developed caecae (Table VI). In the other species the mean of six caecae must significantly increase the surface area of the intestinal epithelium. This is probably the major function of pyloric caecae in fish (Barrington, 1957).

The dentition of the four species studied microscopically seems to be ideally adapted to cope with the specific natural diet of each species (Fig. 7). The blunt and relatively small teeth of *Liza dumerili* (Fig. 7 and Smith, 1935) are ideally suited to ingest relatively coarse sandy substrate. On the other hand the sharp pointed teeth of *L. richardsoni* and especially *Mugil cephalus* (Fig. 7 and Van der Elst & Wallace, 1976) would enable these species to select fine material. The relatively large tricuspid teeth, with sharp cutting edges, of *Liza tricuspidens* (Fig. 7, Smith, 1935 and Van der Elst & Wallace, 1976) would be essential to dislodge and reduce attached diatoms, filamentous algae and pieces of macro-plant detritus in size prior to ingestion. Blaber (1973) conclusively showed that dentition of *Rhabdosargus holubi* was related to and changed in accordance with the type of diet ingested. Thomson (1954) also commented on the relatively weak teeth of the family Mugilidae. He found that those species ingesting diets with more animal food had better developed teeth. From the food preferences of four species from the Swartkops estuary, however, it seems that species ingesting coarser plant and algal material, had better developed teeth.

The present studies show that the dominant mullet species in the Swartkops estuary not only exhibited different feeding periodicities (*Liza dumerili* and *L. richardsoni*) but selected material in all the species differed in chemical as well as physical properties. Alimentary canals of each species are morphologically well adapted for selection, ingestion and digestion of its preferred food items. These factors reduce interspecific competition among mullet species, especially if they utilise the same environment as is often found in the Swartkops. In contrast to the

Swartkops, co-existence and sharing of the same food resources were found for certain mullet species in St Lucia (Blaber, 1976) and in the Pullamandam Lagoon, India (Luther, 1962). Blaber (1976) explained that this sharing of food resources and co-existence may possibly be due to superabundance of certain foods.

Acknowledgements

Grateful acknowledgement is paid to the University of Port Elizabeth and the Department of Environmental Planning and Energy for financial support, Mrs. L. Botha for drawing the figures, Mrs. M. Joubert for typing and Mr. R. Randall for critically reading the manuscript.

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J. exp. mar. Biol. Ecol., 1980, Vol. 44, pp. 211–228
© Elsevier/North-Holland Biomedical Press

POPULATION DYNAMICS, GROWTH AND REPRODUCTIVE RATES OF *LITTORINA NIGROLINEATA* Gray FROM A MODERATELY SHELTERED LOCALITY IN NORTH WALES

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Abstract: The population dynamics of *Littorina nigrolineata* Gray on a moderately sheltered boulder shore was characterized by an almost constant mortality rate of post-juvenile snails both within and between years. Cohorts of post-juvenile snails had a "half life" of about 5 months. Juvenile snails had higher mortality rates than post-juveniles. Mortality rate was independent of size in post-juveniles. The population of post-juvenile snails fluctuated only about two-fold during the 3 yr of study. Maxima of population size occurred each September as a result of an autumnal pulse of recruitment into the post-juvenile size classes. These recruits originated from eggs laid in the summer of the previous year. The size-frequency structure of the population lacked well defined modes except during the spring and summer when the pulse of recruits formed a distinct mode, which later disappeared due to growth and mortality of the recruits. Oviposition continued throughout the year with a pulse in summer. Newly laid eggs took 4–7 wk to hatch. The hatchlings had a mean shell height of 0.5 mm and were estimated to take 6–9 months to grow to a shell height of about 4 mm. Growth increments over periods of 3 months, estimated from tagged cohorts of snails ranging from 3 to 16 mm, released on a stone jetty, revealed seasonal and size-specific changes in growth rate. Growth rate was significantly lower between December and March than at other times of the year. Seasonal differences in growth rate did not, however, significantly affect the yearly size increments of snails hatching in summer or winter. Growth increments did not decline linearly with increasing body size, as is assumed by the von Bertalanffy growth model, but increased to a maximum at about 6–7 mm shell height. Beyond the maximum, the growth increments decreased linearly with increasing shell height. This non-linearity caused an inflexion in the growth curve, so that the shell height at 2 yr of age was predicted to be 9.8 mm by the inflected growth curve and 12.4 mm by the von Bertalanffy growth curve. The deviation from the von Bertalanffy growth model was possibly due to departures from the assumptions that the assimilation rate is proportional to the square of a linear size dimension and that the metabolic rate is proportional to the cube of the same dimension. A von Bertalanffy growth curve, fitted to growth increments measured from "growth checks" on tagged snails on the boulder shore, predicted slightly faster growth rates than the von Bertalanffy growth curve fitted to increments of mean cohort size on the stone jetty. The closeness of the two curves, however, suggested that both methods of measuring growth increments were tolerably accurate.

INTRODUCTION

This paper presents the first published data on the population dynamics, growth, and reproductive potentials of *Littorina nigrolineata* Gray, being part of a more comprehensive study of the comparative demography of *Littorina* spp. in North Wales (Hughes & Roberts, in prep.). The data include temporal changes in population size and size-frequency structure, snail survival, growth rates, and seasonal changes in spawning activity. Also, the effectiveness of using "growth checks", in-

duced by handling the snails, as markers for measuring growth rates is evaluated by comparing the resulting growth estimates with those obtained from changes in the mean shell size in cohorts of tagged snails. The adequacy of the von Bertalanffy growth equation as a detailed model of littorine growth is tested by examining the relationship between short-term growth increments and snail size.

Littorina nigrolineata was described as a distinct species from *Littorina rudis* Maton 1797, by Gray (1839). Subsequently, *L. rudis* and *L. nigrolineata* were designated as forms of *L. saxatilis* Olivi 1792, by Dautzenberg & Fischer (1912), a point of view upheld by James (1968). The recent works of Heller (1975), Caugant (1979), and Raffaelli (1979) leave little doubt, however, that *L. nigrolineata* represents a distinct species within the *L. saxatilis* species complex. *L. nigrolineata* can be distinguished from *L. rudis* by its relatively more rounded, more robust shell which is sculptured by rather broad flattened ridges along the whorls. The colour of the shell tends to be uniform with no patterning except for the thin black lines between the ridges present in some morphs. The colour is commonly yellow or off-white, but may vary according to the colour of the rocks. For example, at Dale, Pembrokeshire, purple-red morphs matching the sandstone coexist with the more widespread yellow morphs, while at Roscoff, Brittany, yellow-brown morphs and blueish-white morphs match the local rock colour (pers. obs.). *L. nigrolineata* may be found on moderately to fully exposed shores from about M.L.T.L. to M.H.W.N., usually coexisting with *L. rudis*. Shell thickness tends to increase with increasing shelter of the shore as does that of *L. rudis*. The thinnest *L. nigrolineata* from fully exposed shores are of about the same thickness as the thickest *L. rudis* from more sheltered shores (Elner & Raffaelli, 1980). *L. nigrolineata* is oviparous, laying egg masses beneath stones and in damp crevices. Most forms of *L. rudis* are ovoviviparous, but at least one form, recently designated as a separate species, *L. arcana*, by Hannaford-Ellis (1978) is oviparous and lays egg masses similar to those of *L. nigrolineata* (pers. obs.).

Methods

Sites studied

The sites studied were a moderately sheltered boulder shore, Lewis (1964) exposure rating 3–4, at Trwyn-y-Penrhyn, Anglesey (SH 629 797) and a stone jetty adjacent to Bangor Pier (SH 584 733) which is rather more sheltered than the boulder shore. The two sites are 7.5 m apart and their populations of *L. nigrolineata* are completely isolated from each other.

The shore at Trwyn-y-Penrhyn has a moderate gradient and is covered with a very wide size range of stones derived from the erosion of glacial moraine. The largest boulders weigh several tons and are completely static, but moderately sized

boulders and smaller stones are rolled about by waves in stormy weather. The underlying substratum is boulder clay, but this is covered by a heterogeneous collection of gravel and pebbles, the depth of which varies considerably from time to time due to transportation in rough weather. *L. nigrolineata* and *L. rudis* sheltering beneath boulders are often covered by several cm of gravel after a storm. At other times the gravel may be scoured away, revealing the underlying clay. *L. rudis* is very dense from E.H.W.S. down to the upper edge of the *Ascophyllum nodosum* (L.) Le Jol. zone, just below M.H.W.N., but continues at lower densities right through the *Ascophyllum* zone down to a level somewhat above M.L.W.S. where the gradient levels off and the substratum changes to silty sand sparsely covered with stones. *Littorina nigrolineata* occurs at higher densities than *L. rudis* from the upper edge of the *Ascophyllum* zone down to where the boulders give way to muddy sand. Within this zone, the density of *Littorina nigrolineata* varies according to the availability of suitable stones beneath which to shelter. During low tide, most *L. nigrolineata* are found sheltering beneath stones, but a significant proportion of them remain quiescently on the sides of boulders, and in this respect seem to differ from *L. rudis*, very few of which remain out on open surfaces when not foraging. There is no detectable segregation of age groups on this shore, juveniles and adults are usually found together beneath the same stones. There is a tendency, however, for juveniles to shelter among barnacles on the sides of the larger boulders, whereas adults are uncommon in this microhabitat. *L. nigrolineata* tend to be less abundant among stones with the densest growths of *Ascophyllum*, perhaps because these stones are the most stable, being deeply embedded in the substratum, so that snails cannot crawl and shelter beneath them. Also, perhaps foraging is more difficult among dense growths of *Ascophyllum*. Only exceptionally are *Littorina nigrolineata* found on fucoid fronds. *L. nigrolineata* also tend to be absent from large cavities beneath stones which shelter shore crabs, the latter being predators of *L. nigrolineata* (Elner & Raffaelli, 1980).

The stone jetty adjacent to Bangor pier juts at right angles to the southwest–northeast axis of the Menai Strait. Strong currents impinge on both sides of the jetty, depending on the state of the tide. *L. nigrolineata* are found mainly on the southwestern face of the jetty, which is shaded from the sun to some extent by the adjacent pier and which is subjected to moderate wave action generated by the prevailing southwesterly winds. Mortar between the large rectangular stones of the jetty has been eroded away, leaving deep cavities within which *L. nigrolineata* shelter during high tide and when the substratum dries out during low tide. The stones are colonized by barnacles, the density of which increases towards the seaward extremity of the jetty. At the landward extremity of the jetty, corresponding to about M.H.T.L., *L. nigrolineata* are replaced by *L. rudis*. Very few *L. rudis* extend into the main *L. nigrolineata* population.

ESTIMATIONS OF POPULATION SIZE, POPULATION SIZE-FREQUENCY STRUCTURE, AND SURVIVAL

Population density at Trwyn-y-Penrhyn was estimated from mark-recapture samples taken every 3 months from July 1976 to September 1979. To do this, a 10-m wide strip of shore extending from M.H.W.N. to M.L.W. (15 m) was searched for 1.5 h on each sampling occasion. All movable stones were upturned and replaced and all accessible crevices and surfaces covered by seaweed were examined. Quadrat sampling would have been impossible in this habitat because many snails were inaccessible in deep crevices or beneath immovable boulders. The number of snails collected in 1.5 h was also anticipated to be unreliable as an estimate of population size because sampling efficiency was likely to have varied due to temporal differences in weather conditions and in the amount of gravel and pebbles present between the boulders.

Initially, all snails identifiable as *L. nigrolineata* were brought back to the laboratory for measuring and marking, but after September 1976, snails <4 mm height (base to apex) were ignored because sampling them was found to be too inaccurate. In the laboratory, the snails were measured with vernier calipers for the construction of size-frequency diagrams and marked by making a shallow pit above the outer lip of the shell using a dental drill. The pit was then painted with Humbrol cellulose paint, allowed to dry on the laboratory bench for 24 h, and then returned to the shore. The snails were colour coded according to date of capture, snails accumulating several colour dots as they were recaptured. Initial trials, where marked snails were kept in aquaria, showed that the marking procedure did not cause a significant amount of mortality. Also, several snails in the population survived over 2.5 yr and accumulated five to six tags. After each sampling occasion, the data were tabulated to show the history of recapture of each snail in the sample. In this way, account could be taken of snails which were missed on one occasion, but recaptured in a later sample. Finally, a trellis table was constructed (Table I), the first column representing the number of snails captured on successive dates, the second column representing the number of releases on successive dates (a few snails were lost or killed by accident in the laboratory) and the remaining successive columns listing the recapture histories of cohorts of snails released on successive sampling dates. Estimates of population size were then made from the trellis table using the Fisher–Ford method, programmed in ALGOL by Bishop & Sheppard (1973). For the purposes of computation, separate trellis tables were constructed for the periods September 1976 to September 1978 and September 1977 to September 1979. The July–August 1976 data were omitted because they included small juvenile snails not included in later samples. The Fisher–Ford calculations for the entire data from September 1976 to September 1979 were found to be unreliable, being sensitive to the extinction of cohorts beginning in September 1978 (Fig. 3). The two sets of 1976–1978 and 1977–1979 data gave very similar estimations

of population size for the period of overlap in 1977, thus vindicating this way of analysing the data. The snails from Trwyn-y-Penrhyn were not given specific individual marks so that size-specific survival could not be estimated from the mark-recapture data. The data in the trellis table represent average survival for all sizes of snail in the samples. To check on the possible variation in survival with snail size, a population where the recapture of snails was more efficient had to be found. A satisfactory population was found on the stone jetty adjacent to Bangor pier. The jetty population of *L. nigrolineata* had a size-frequency structure similar to that of the Trwyn-y-Penrhyn population, suggesting that size-specific mortality rates and growth rates were probably similar in the two populations. It was found that very high proportions of tagged snails could be recaptured on the jetty by collecting snails which were foraging over the open surfaces on the receding tide and repeating this on three to four successive tides. The recapture efficiency on the jetty was very much higher than at Trwyn-y-Penrhyn because the jetty masonry presented a simpler topographical surface which was much more easily scanned and was more accessible than that at Trwyn-y-Penrhyn. Cohorts of 20–70 snails in successive 1-mm shell height categories, with pivotal sizes of 3.5–16.5 mm, were colour-coded according to size category and date of release. After drying the paint for 24 h, the snails were replaced carefully within crevices in the masonry. Snails were recaptured 3 months later and their shell heights measured. The recaptured snails were re-sorted into 1-mm size categories, and supplemented with newly captured snails to make up new cohorts. These cohorts were given new colour codes indicating size category and date of release. This procedure was repeated in September 1977, December 1977, March 1978, and June 1978. From these data, survival could be estimated as a function of size and of season.

ESTIMATION OF GROWTH RATES

The recapture efficiency at Trwyn-y-Penrhyn was too low for it to be worthwhile uniquely tagging individual snails for growth measurements. Instead, growth increments of the tagged cohorts from Bangor jetty (see above) were used to estimate growth rate as a function of snail size and of season. Growth curves spanning a 5-yr period from birth were constructed directly from these estimations. Some of the recaptured snails at Trwyn-y-Penrhyn, however, developed discernible growth checks after handling, so that growth increments between successive captures could be measured. These growth increments were used to estimate the parameter k (instantaneous size specific growth rate) of the von Bertalanffy equation (Fig. 6) after assuming that the *L. nigrolineata* reached an asymptotic size of 18 mm. The von Bertalanffy equation was then used to predict a growth curve for comparison with that derived directly from the Bangor jetty data. A von Bertalanffy growth curve was also fitted to the Bangor jetty data by estimating k as the slope of the linear portion of height increment on initial shell height (Fig. 5) and by assuming an asymptotic height of 18 mm.

Embryonic development rates were measured by enclosing newly laid egg masses in clear plastic 9 × 1.5 cm tubes with perforated lids and plankton netting "windows" near the base. The tubes were wedged in crevices in the masonry of Bangor jetty and periodically inspected to ensure free drainage of the tubes and to check the development stage of the embryos. Tubes were put out in April, June, August, and December 1978. The December sample later disappeared unaccountably. Size at birth was measured for samples of hatchlings in the April batch.

ESTIMATION OF FECUNDITY

Ten each of pre-sexed mature male and female *L. nigrolineata* were kept in a stainless steel wire mesh cage at Trwyn-y-Penrhyn. The cage had a 2-mm mesh constructed of very robust stainless steel wire which was riveted to a stout angle-iron frame 60 cm square by 50 cm deep. The cage was fitted with a hinged lid for easy access and was wedged between two large boulders in the upper third of the *L. nigrolineata* zone. The bottom of the cage was covered by about 15 cm of gravel and pebbles, on top of which were placed about a dozen stones ≈15 cm in diameter. On top of these rested two very large stones, occupying most of the available area. These large stones had very pitted undersurfaces, chosen so as to be attractive oviposition sites for *L. nigrolineata*. Each month from November 1976 to July 1977 and from September 1977 to June 1978, egg masses were collected from the large stones. Occasional egg masses were also found on the smaller stones or in the angle-iron corners of the cage. The adult snails were counted and measured on each occasion. Small crabs were removed to prevent predation on the egg masses. In the laboratory, the egg masses were dissected into small pieces under the binocular microscope and the number of eggs per egg mass counted using a digital counter and a channelled piece of perspex to arrange the egg mass fragments into a linear array.

RESULTS

POPULATION SIZE

After an initial drop from 1213 to 277 in July–August 1976, which was largely due to the inadequate sampling of juveniles <4 mm in height, the total number of snails captured on each date (Table I) remained remarkably steady, the maximum in September 1977 exceeding the minimum in March 1979 only by a factor of 3.4 (Fig. 1). Population size estimated by the Fisher–Ford method was usually two to three times the sample size on each date and fluctuations in estimated population size followed a similar pattern to fluctuations in sample size (Fig. 1), suggesting that sampling efficiency must have been less variable than anticipated. The maximum estimated population size in December 1977 exceeded the minimum in September 1979 by a factor of 2.3.

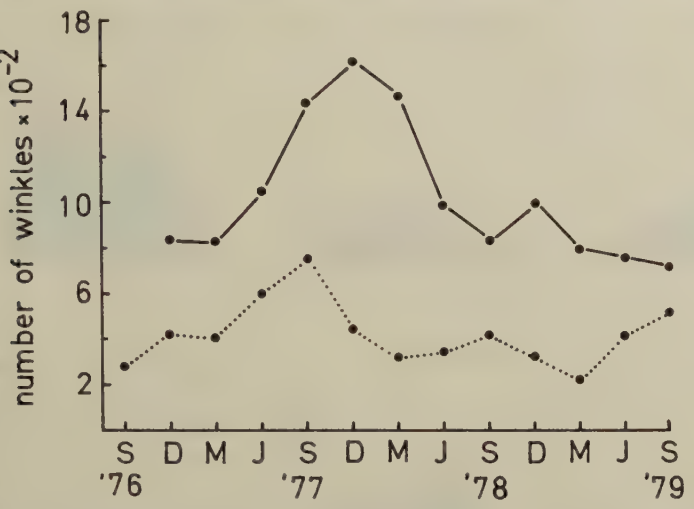

Fig. 1. Changes in population size over 3 yr: the solid line represents Fisher-Ford estimations of total population size from the mark-recapture of *L. nigrolineata* at Trwyn-y-Penrhyn; total population size can be converted to number per m^2 by dividing by 150; the dotted line represents the total number of captures on each sampling occasion.

POPULATION SIZE-FREQUENCY STRUCTURE

The population size-frequency structure, estimated from the mark-recapture samples at Trwyn-y-Penrhyn, was rather featureless, lacking distinct modes for much of the year (Fig. 2). This was due to the continuous recruitment of juveniles and continued shell growth throughout the year. The greater oviposition rate in the summer, however (Fig. 8), caused a mode to appear among the 4- to 6-mm size classes from March to July in the following year. By September this mode had merged completely with the larger size classes owing to growth of the snails and to the declining recruitment rate in the autumn.

SURVIVAL

Estimates of cohort size on successive sampling occasions, derived from the mark-recapture data with corrections made for snails which were missed on some occasions but recaptured later, are plotted on a semi-log scale in Fig. 3. In July and August 1976, the population was stratified into upper, middle, and lower sections, the snails being given different colour codes for each section. This procedure was abandoned in September 1976 because it was apparent that there was no detectable difference in survival among the three shore levels (Fig. 3). Mortality within the July and August 1976 cohorts was much greater in the first month or two after release than in the remaining period (Fig. 3). This was due to the inclusion of small (<4 mm) snails in the cohorts. Recovery of such small snails was very low, partly

TABLE I

Recapture histories of tagged cohorts of *L. nigrolineata* released at Trwyn-y-Penrhyn.

Date	Total no. captured	Total no. released															
15 July 1976	1213	1189	July 1976														
22 July 1976	1022	1018	390	July 1976													
26 Aug. 1976	816	806	240	269	Aug. 1976												
20 Sept. 1976	277	275	60	86	82	Sept. 1976											
16 Dec. 1976	405	401	54	75	81	74	Dec. 1976										
21 March 1977	402	392	31	48	51	52	99	Mar. 1977									
27 June 1977	605	590	13	28	37	30	86	111	June 1977								
20 Sept. 1977	758	748	14	13	35	19	57	56	158	Sept. 1977							
31 Dec. 1977	426	411	8	9	9	8	16	23	37	94	Dec. 1977						
20 March 1978	322	319	3	2	3	2	4	3	20	61	44	Mar. 1978					
29 June 1978	348	333	2	0	6	2	4	5	14	55	34	72	June 1978				
14 Sept. 1978	414	389	0	0	1	1	2	2	16	33	22	49	114	Sept. 1978			
20 Dec. 1978	307	292	0	0	0	0	1	0	3	5	12	22	35	65	Dec. 1978		
23 March 1979	226	214	0	0	0	0	1	1	5	11	4	15	24	32	35	Mar. 1979	
16 June 1979	407	392	0	0	0	0	1	1	2	9	7	9	26	33	48	62	June 1979
16 Sept. 1979	524	–	0	0	0	0	0	0	0	1	0	11	23	37	24	56	155

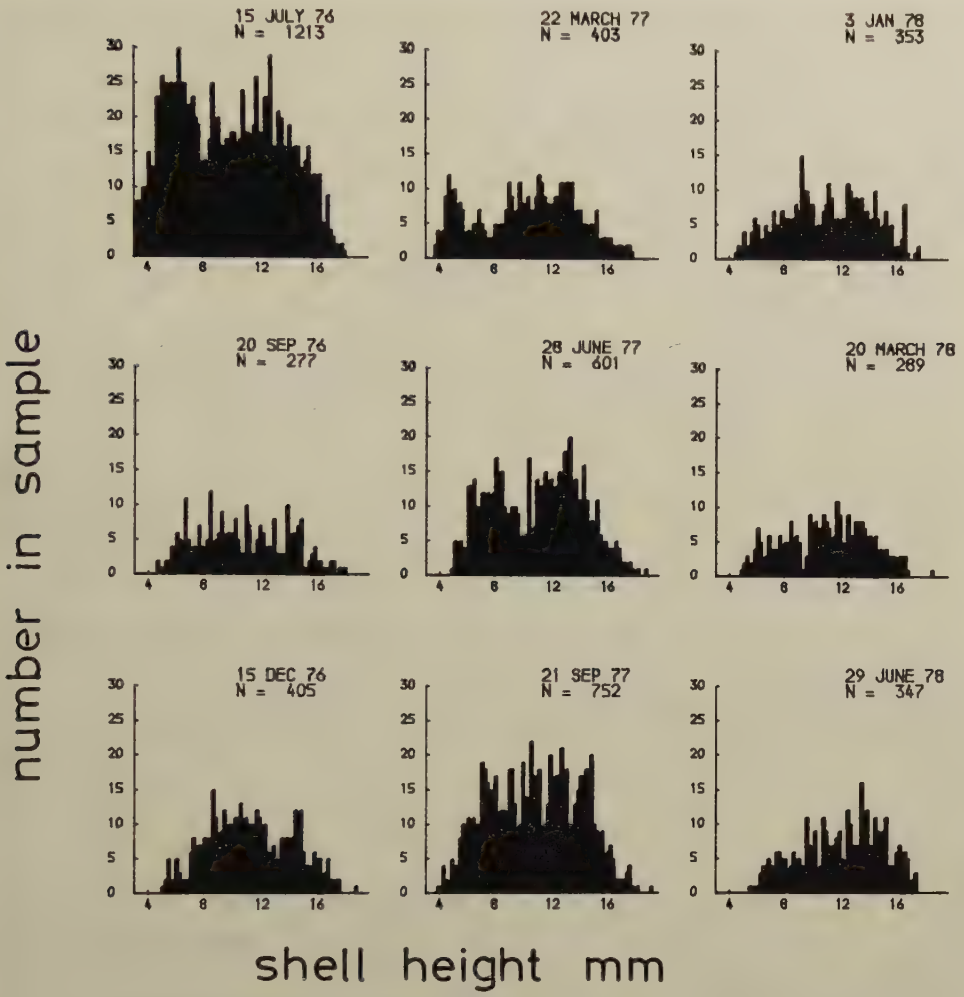

Fig. 2. Size-frequency histograms for the population of *L. nigrolineata* at Trwyn-y-Penrhyn: the size classes represent intervals of 0.2 mm.

because of the greater size-specific mortality of small snails (Fig. 4) and partly because the marks tended to become covered over by the growing shell, so that recaptured snails were mistaken for new captures. Survival among cohorts released on each sampling occasion from September 1976 was remarkably constant, with no detectable fluctuations caused by the movement of the substratum during equinoxial gales (Fig. 3).

Estimations of survival for snails >7 mm on the Bangor jetty were rather erratic (Fig. 4) and were not significantly correlated with snail size. The mean estimated survival of *L. nigrolineata* >7 mm shell height was 0.61 per 3 months, and was

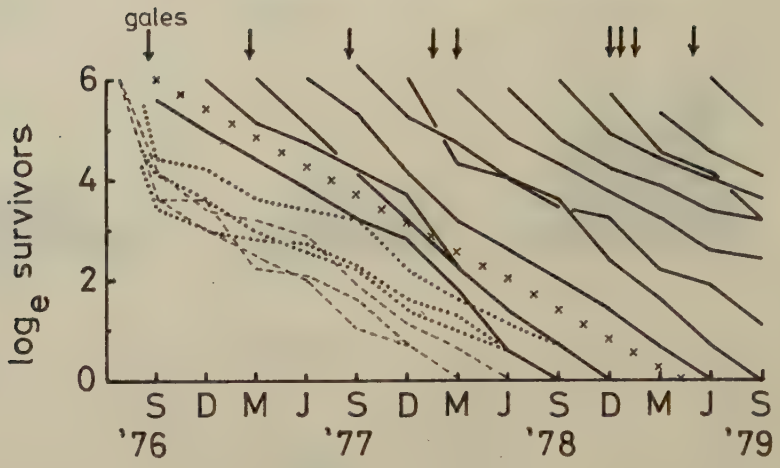

Fig. 3. Survivorship curves for cohorts of tagged *L. nigrolineata* released at Trwyn-y-Penrhyn: the dashed and dotted lines represent cohorts released at three shore levels in July 1976 and August 1976, respectively; the remaining cohorts (solid lines) were captured from and released throughout the whole area studied; the crosses represent the survivorship estimated by the Fisher–Ford program.

quite close to the survival of 0.57 per 3 months estimated for the Trwyn-y-Penrhyn snails by the Fisher–Ford program. Estimations of survival for the Bangor jetty snails decreased very markedly at shell heights <7 mm, the estimated survival of 4-mm snails being only about 0.15 per 3 months (Fig. 4). The survival of snails of all sizes

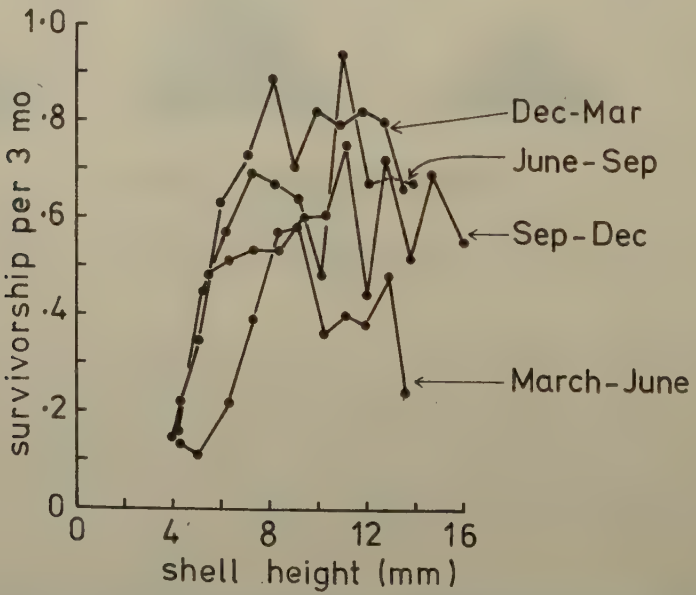

Fig. 4. Survivorship per 3 months of different sized snails, estimated from cohorts of tagged *L. nigrolineata* released on Bangor jetty at different times of the year, plotted against initial shell height.

on Bangor jetty was lowest during the period March to June and highest during December to March (Fig. 4).

GROWTH

Three-monthly growth increments of the Bangor jetty snails are plotted as a function of initial shell height in Fig. 5. Beyond a shell height of ≈7–8 mm, the growth increments decreased linearly with increasing initial shell height. This linear relationship did not hold for snails smaller than ≈7–8 mm. In these smaller snails there was a tendency for growth increments to increase as initial shell height increased, but the data were inadequate to rule out the possibility that growth increments were independent of size below a shell height of 7–8 mm. Cohorts of snails larger than about 14 mm were too small for the reliable estimation of three-monthly growth increments, but after 12 months the few survivors in this size range had each grown by an amount predicted for a 3-month period by extrapolation from the data on smaller snails (Fig. 5).

Growth increments for all sizes of snail were significantly lower for the period December to March, but there was no significant variation in growth rates over the spring, summer, and autumn (Fig. 5).

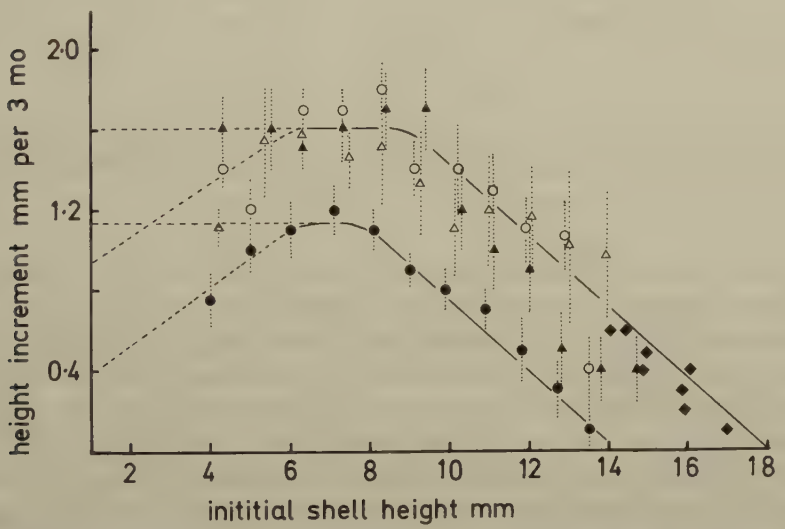

Fig. 5. Increments in shell height per 3 months plotted as a function of initial shell height for *L. nigrolineata* on Bangor jetty: vertical dotted lines are standard errors; ●, December–March 1978; ○, March–June 1978; △, June–September 1978; ▲, September–December 1977; ◆, annual increments of large snails September 1977–September 1978; the curves represent the functions relating height increment to initial shell height used to construct the "direct" growth curves in Fig. 6; the upper curve represents "summer" growth and the lower curve "winter" growth; the dashed portions represent the alternative assumptions of an independent (horizontal) or positive (rising) relation between height increment and initial shell height.

The parameter k of the von Bertalanffy growth model, estimated from the Trwyn-y-Penrhyn growth-check data, was found to be independent of initial shell height (Fig. 6), this independence being a prerequisite of the von Bertalanffy model. The von Bertalanffy growth curve fitted to the Trwyn-y-Penrhyn data predicted slightly faster growth than the one fitted to the Bangor jetty data (Fig. 7).

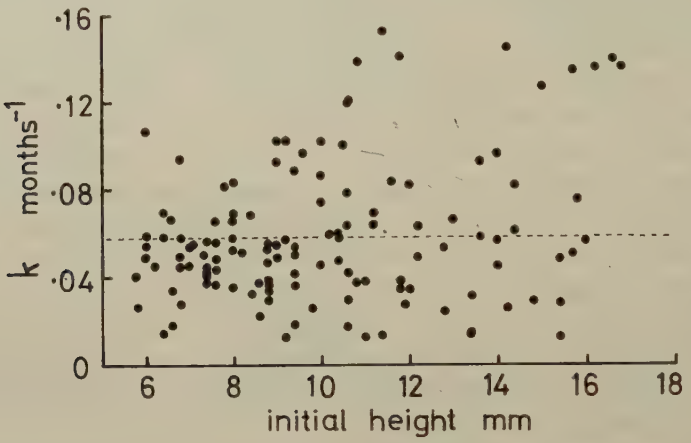

Fig. 6. The parameter k of the von Bertalanffy growth equation plotted against initial shell height for the growth-check data from Trwyn-y-Penrhyn: the dotted line represents the mean value of k which was used to generate the corresponding growth curve in Fig. 7; the individual values of k were derived by using a re-arrangement of the von Bertalanffy equation:

$$k = \frac{1}{t_2 - t_1} \cdot \log_e \left[\frac{h_\infty - h_1}{h_\infty - h_2} \right],$$

where h_1 and h_2 are the shell height at and beyond the growth check, respectively, h_∞ is the asymptotic shell height, $t_2 - t_1$ is the time elapsed between the release date when the growth check is assumed to have been formed and the time of recapture.

Eggs kept in plastic tubes on Bangor jetty hatched after about 7 wk when put out in April and June and after about 4 wk when put out in August. There was, however, a considerable variation in the hatching time among embryos from the same egg mass. Embryos put out on 10 April showed signs of hatching on 22 May, 3 had hatched on 24 May, 20 had hatched on 28 May, about three-quarters of the total had hatched on 1 June, and on examining the egg mass in the laboratory on 2 June, 157 embryos were found to have hatched, leaving 20 unhatched embryos in the centre. Hatching had, therefore, been spread over at least 10 days. The mean shell height of hatchlings, measured under a binocular microscope equipped with a graticule, was 0.50 mm, SE = 0.005, $n = 20$.

FECUNDITY

Eggs were laid in all months of the year, with a marked peak in May–June (Fig. 8). Each egg mass contained ≈100–200 eggs. Egg masses which appeared to contain

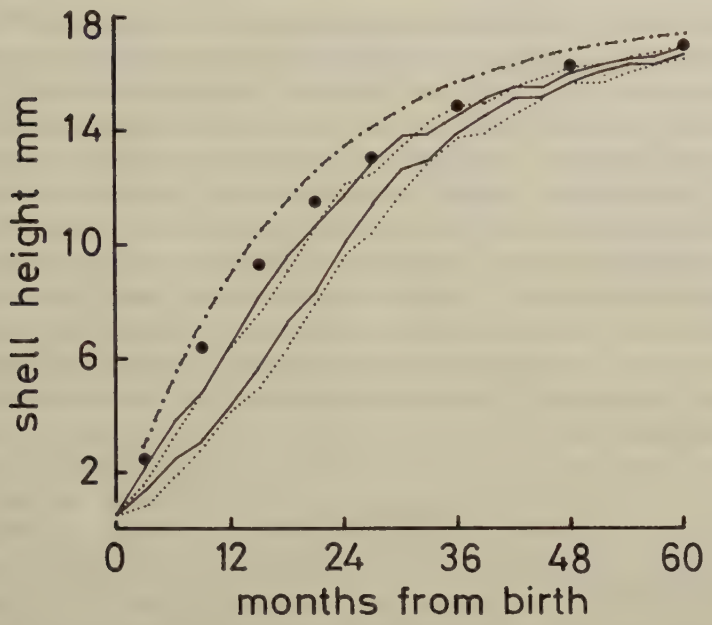

Fig. 7. Growth curves for *L. nigrolineata*: the solid and associated dotted curves represent growth estimated "directly" from the observed relation between height increment and initial shell height depicted in Fig. 5; growth rates appropriate for "summer" and "winter" were applied alternately; the solid curves represent snails hatching in June September and the associated dotted curves represent snails hatching in December–March; the lower pair of curves are derived from a positive relation between height increment and initial shell height of small (<6 mm) snails, and the upper pair of curves are derived from an independent relationship between these variables. Above the "direct" growth curves are the von Bertalanffy growth curves for Bangor jetty (●) and Trwyn-y-Penrhyn (–·–·–).

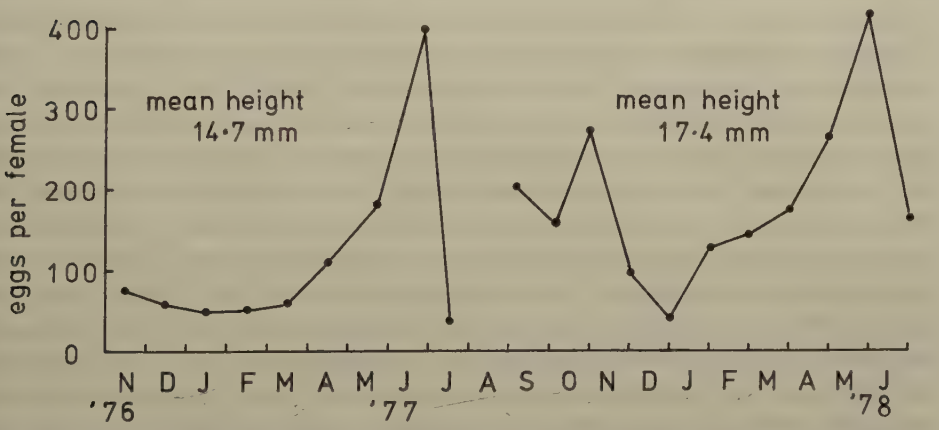

Fig. 8. Seasonal oviposition rates per female *L. nigrolineata* kept in a wire-mesh enclosure at Trwyn-y-Penrhyn: the total number of eggs laid by the 1976–1977 and 1977–1978 batches were 1028 and 2080, respectively.

>300 eggs were probably two separate egg masses laid contiguously. This was a common phenomenon, usually recognizable because of the different developmental stages of the embryos in the different egg masses. Shell growth of the adults occurred in both the November 1976 to July 1977 batch and in the September 1977 to June 1978 batch. The mean shell heights of the two batches half-way through the experimental periods were 14.7 and 17.4 mm, respectively. There was some evidence that the batch of larger snails was more fecund than the batch of smaller snails (Fig. 8), the mean number of eggs laid per female from December to June inclusive being 914 for the smaller snails and 1272 for the larger snails. Three males and four females in the 1976–1977 batch and three females in the 1977–1978 batch died during the period of study. One of the surviving females in the 1977–1978 batch was parasitized by trematodes. These factors were taken into account in the calculation of fecundity per female.

Discussion

POPULATION DYNAMICS

The substratum at Trwyn-y-Penrhyn is very unstable and during storms there is considerable shifting of stones up to the size of moderate boulders, so that crushing by moving stones would seem likely to be a relatively large mortality factor among the resident populations of *L. nigrolineata* and *L. rudis* (Raffaelli & Hughes, 1978). It is surprising, therefore, to find no evidence of increased mortality due to stormy weather from the mark-recapture data for Trwyn-y-Penrhyn (Fig. 3). The substratum of Bangor jetty is, by contrast, perfectly stable, yet the mortality rate estimated from the mark-recapture data for post-juvenile snails is only 7% less than that for post-juveniles at Trwyn-y-Penrhyn. The "half-lives" of tagged cohorts, calculated as $\log_e 0.5/(-\text{mortality rate})$, were 4.8 months for Trwyn-y-Penrhyn and 5.3 months for Bangor jetty. A possible source of mortality at Bangor jetty was dislodgement by wave-action, but this seems likely to have been small because snails dropping to the foot of the jetty became lodged among fucoids and stones and were able to climb back onto the jetty wall (pers. obs.). Large populations of shore crabs, *Carcinus maenas* (L.), forage throughout the *Littorina nigrolineata* zone both at Trwyn-y-Penrhyn and the Bangor jetty. Shore crabs are able to feed on *L. nigrolineata* in the laboratory (Elner & Raffaelli, 1980) and the frequent presence of broken empty shells and snails with repaired shells in the field were taken by Heller (1976) and Raffaelli (1978) as evidence of crab predation. Unfortunately, injuries caused by crabs or by impacts with moving stones are indistinguishable (pers. obs.), so that the importance of crab predation on *L. nigrolineata* in the field remains to be evaluated directly. Crab predation is, however, evidently a feature common to Trwyn-y-Penrhyn and Bangor jetty and if important, might account for the similar mortality rates of post-juvenile *L. nigrolineata* on both shores.

Total population size excluding small juveniles, estimated from the mark-recapture data using the Fisher–Ford method of analysis, remained relatively stable with only about a two-fold maximum change during the 3 yr of study. Estimations of density are not very meaningful for a habitat as heterogeneous as the shore at Trwyn-y-Penrhyn. Snails were very patchily distributed, following the distribution of suitable shelter sites under stones. The figures for population size given in Fig. 1 can, however, be converted to densities by dividing them by the area of beach sampled. This gives a maximum estimated population density of 11 per m^2 for December 1977 and a minimum of 5 per m^2 for September 1979. The Fisher-Ford estimations of population size are likely to have been quite accurate because the assumptions of the method were met, namely, random mixing of marked with unmarked snails, equal capturability of marked and unmarked snails, and equal survival of marked and unmarked snails. There is evidence that the proportion of recaptures of marked snails was less after the first period of release than after subsequent periods (Fig. 3), possibly due to mortality induced by tagging or due to the loss of imperfect tags. This effect was slight and had a negligible effect on the calculation of survival by the Fisher–Ford procedure. Indeed, the Fisher–Ford estimation of survival fitted the observed individual survival curves very closely (Fig. 3). The proportion of tagged snails in the population estimated by the Fisher-Ford procedure ranged from 18% after the first period of release to 59% after the last period of release, suggesting that between a third and a half of the population must have been captured on most occasions. Adjacent areas of beach were searched on several occasions and from the marked snails recovered in these areas, it was estimated that less than 1% of the apparent mortality of tagged cohorts was due to emigration. Similar amounts of emigration occurred on both sides of the "population" so that the emigration of marked snails was probably equal to the immigration of unmarked snails. The resulting slight dilution of marked snails within the "population" would have had a minimal effect on the estimations of population size.

As plotted in Fig. 1, the Fisher–Ford estimations of total population size are one sampling period out of phase with the plot of actual sample size. This is a computational artefact and when interpreting changes in population size, the Fisher–Ford plot should be shifted one sampling period to the left. The large peak of estimated population size in December 1977 should, therefore, represent a true peak in September 1977, coincident with the peak in sample size. This peak was probably due to a heavy autumnal pulse of recruitment since a similar, but much smaller peak, was seen in September 1978. Evidence of a peak in September 1979 was present in the plot of sample size, but the Fisher-Ford plot continued to decline over this period (Fig. 3), possibly due to a computational artefact which would have been rectified with a further series of samples. The interpretation of the peaks as autumnal pulses of recruitment is corroborated by the occurrence of a summer pulse of oviposition (Fig. 8). Because *L. nigrolineata* eggs take $\approx$1.5 months to hatch and the juveniles take $\approx$9–12 months to grow to a shell height of $\approx$6 mm (Fig. 7), the recruitment

peaks in Fig. 1 correspond to summer pulses of oviposition in the previous year. A similar late summer pulse of recruitment was recorded in several populations of *L. rudis* by Roberts & Hughes (in prep.).

GROWTH

The growth data cover the hatching period of the eggs and growth beyond a shell height of 3 4 mm, the smallest mean cohort size used at Bangor jetty. An attempt to measure the growth rate of hatchlings in the laboratory was abortive due to accidental loss of the snails. The growth rates of hatchlings estimated by horizontal extrapolations of the height increment curves in Fig. 5 do, however, agree with observed growth rates of juvenile *L. rudis* (Roberts & Hughes, in prep.).

Fig. 5 shows that there is a distinct non-linearity in the function relating height increment to initial shell height. The data suggest that height increments increase as initial shell height increases up to $\approx$6-7 mm, but do not obviate the possibility that height increments are independent of initial shell height over this size range. Both possibilities lead to an inflexion of the growth curve, the inflexion being more pronounced when size increments increase as initial shell height increases up to 6–7 mm (Fig. 7). Peaked curves of growth increment plotted against initial size have also been recorded in *Cerithium nodulosum* (Yamaguchi, 1977), in *Monodonta lineata* (Williamson, pers. comm.) and in *Cepaea nemoralis* (Williamson, 1976). The von Bertalanffy growth model used in the present paper assumes that growth increment is a linear function of initial size with negative slope. This assumption is based on two further assumptions that the assimilation rate is proportional to the square of a standard linear dimension of the body and that the metabolic rate is proportional to the cube of the same linear dimension. Departures from either of these assumptions will cause the size increment – body size function to be non-linear. Metabolic rate is proportional to length raised to a power <3.0, usually near 2.25 (Hemmingson, 1960). The relationship between assimilation rate and body size has not been adequately studied for any generalizations to be made. On these theoretical grounds alone, however, non-linear growth increment – body size functions are to be expected (von Bertalanffy, 1960). Changes in body proportions and embryological organization might also produce non-linearities, but shape remains constant in *Littorina nigrolineata* beyond a shell height of about 1 mm. "Growth increments" in the von Bertalanffy model are assumed to be instantaneous, as distinct from growth increments over finite periods. Obviously, measured growth increments are finite and they only approximate to instantaneous growth increments when the observation periods become relatively short. Long observation periods, e.g. 1 yr, will tend to obscure the non-linearity in the instantaneous growth increment–body size function because during the observation period, the animal will have grown beyond the non-linear phase, as can be seen by interpolation in Fig. 5. This is why Ford–Walford plots are usually satisfactory for estimating the growth increments of animals over

long time intervals. In the present case, the von Bertalanffy model clearly overestimates the growth rates of small *L. nigrolineata* <6–7 mm shell height, but describes very well the growth beyond this size (Fig. 5). The inflexion due to the non-linearity in the instantaneous growth increment–body size function causes only a slight deviation of the directly constructed growth curve from the von Bertalanffy growth curve if growth increments of small snails are independent of body size, but the deviation becomes quite large if growth increments of small snails increase with increasing body size (Fig. 7). These growth curves converge after about 5 yr of growth, but the estimated sizes at younger ages differ considerably. For example, a 2-yr-old snail is estimated to have a shell height of 12.4 mm by the von Bertalanffy model, and ≈11.8 mm and 9.8 mm by the two "direct" growth curves (Fig. 7). Such differences could be critical in the interpretation of population size-frequency structure or in the construction of life tables from size-specific fecundities and growth rates (Hughes & Roberts, in prep.).

Growth rates were significantly lower during December to March than at other times of year, causing "waves" in the directly estimated growth curves (Fig. 7). Consequently, summer hatchlings will grow to a larger size than winter hatchlings within the first year. As shown in Fig. 7, however, the winter hatchlings catch up with the summer hatchlings after about 12 months and thereafter their respective growth curves diverge and converge seasonally, but this has very little effect on the expected size at a given age for either cohort. There is, therefore, no significant difference between the long-term growth rates of winter or summer hatchlings.

The von Bertalanffy growth curve fitted to the "growth-check" data of marked snails at Trwyn-y-Penrhyn predicts faster growth to the asymptotic shell height of 18 mm than the von Bertalanffy growth curve fitted to the mean size increments of tagged cohorts on Bangor jetty (Fig. 7). The two growth curves are, however, sufficiently close to lend confidence to the two methods of measuring growth increments. The use of "growth checks" induced by the disturbance during capture and tagging is very convenient and does not appear to depress the growth rate over the months subsequent to release. Unfortunately, only about 30% of the snails developed a well-defined "growth-check", so that a large tagging programme is required for this method to yield adequate data.

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SEASONAL RESOURCE PARTITIONING PATTERNS OF MARINE CALANOID COPEPODS: SPECIES INTERACTIONS

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Abstract: *Acartia hudsonica* (Pinhey) and *Temora longicornis* (O. F. Muller) differ in many ways, but they exhibit similar feeding patterns. The quantity of spheres ingested by each species decreased seasonally (fall–summer) and was significantly less in the presence of other species. The food niche width of each species was largest in the fall but decreased and overlapped completely in early summer. These results suggest that *Acartia hudsonica* and *Temora longicornis* are more sensitive than *Pseudocalanus* sp. to temporal variation of the food environment. The niche width of these species was affected both by species interactions and by food levels, with *Acartia hudsonica* being more sensitive to species interactions.

Individuals of *Pseudocalanus* sp. do not respond to seasonal (February–June) changes of the food environment. This is reflected in the narrow food niche width which did not change on a seasonal basis. The average amount of food ingested varied little on a seasonal basis, but increased significantly in the presence of other species. Species interactions with *Temora longicornis* and *Acartia hudsonica* as well as food levels affected niche width and the between phenotype component of niche width.

INTRODUCTION

In what ways and to what extent do co-occurring species differ in their use of food resources? Lokta (1925) and Gause (1934) showed that differences in resource utilization are a necessary condition for coexistence of similar species. Interest in the dynamics of natural communities has resulted in investigations of the quantitative and qualitative aspects of resource utilization by empirical and theoretical ecologists (e.g. MacArthur & Levins, 1967; Diamond, 1970; MacArthur, 1972; Roughgarden, 1972, 1974; Pianka, 1973; Schoener, 1974; Lane, 1975). Numerous investigators have quantified differences between ecologically similar species, but few have attempted to identify food resources and measure directly the way they are apportioned among species.

One method of examining resource allocation is by measuring niche width. The usual definition of niche is any phenotypic attribute of a population of conspecific individuals, or any statistical entity that may change whenever the members of a population change in their response to the environment (Colwell & Fuentes, 1975).

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In this study, niche width is defined as a weighted variance of food size usage (Roughgarden, 1974).

What are the inter- and intraspecific characteristics of food niche width of species which occur together in a variable environment? How are these characteristics related to the seasonal variation of the food environment? In this paper I shall discuss the food usage patterns over a seasonal gradient of food concentration in an attempt to answer these questions. The species studied are *Acartia hudsonica* (Pinhey), *Pseudocalanus* sp., and *Temora longicornis* (O. F. Muller).

Materials and Methods

Particles in a sample of sea water taken at 5 m were counted to determine their number per ml per size category using a Model B Coulter-Counter equipped with 140 and 400 μm apertures. The sea water was diluted by half with Millipore filtered (0.45 μm) sea water and then micronic spheres (3.8, 10, 25, 35, 45, and 55 μm in diameter) were added so that the resulting particle spectrum had approximately the same shape and concentration of particles as the spectrum prior to dilution. The same range of sphere sizes was used for each season. Aliquots of the reconstructed particle spectrum were serially diluted with Millipore filtered sea water to obtain a range of particle concentrations. The greatest particle concentration (no secondary dilution) was designated C_1 and the lowest (4 to 1 dilution) was C_3 (Table I).

Three sets of experiments were performed simultaneously with the reconstructed particle spectrum (Fig. 1). (1) In single species experiments 30 individuals of one species were placed in 250-ml glass bottles containing the reconstructed particle

Table I

Statistics of the experimental particle spectra: m is the average particle diameter; SD is the standard deviation of particle diameter; V is the total concentration of the particle spectrum (PPM).

		m	SD	V
October, 1976	C_1	7.5	21.4	6.6
	C_2	7.2	20.7	2.7
	C_3	6.8	19.5	1.5
February, 1977	C_1	5.1	14.7	1.01
	C_2	5.1	14.6	0.72
	C_3	5.0	14.6	0.41
March, 1977	C_1	6.1	17.5	6.3
	C_2	6.2	17.9	3.4
	C_3	6.5	18.7	2.8
June, 1977	C_1	4.9	14.3	3.8
	C_2	4.3	12.5	3.2
	C_3	4.1	11.9	2.3

spectrum; each treatment was replicated three times. (2) The pairwise species combination experiments were similar to those with single species. Fifteen individuals of each species were placed in each 250-ml bottle; each treatment was replicated six times. (3) For the three-way species experiments 10 individuals of each species were placed in each 250-ml bottle, each treatment was replicated eight times. The bottles were rotated at 2 r/min in the vertical plane in the dark at ambient temperature for 90–120 min. After each experiment the copepods were anesthetized with carbonated water (10 ml/250-ml bottle) and preserved in 4% buffered formalin. Later, the animals were mounted on glass slides, their cephalothorax lengths were measured, and all spheres in the guts of at least 30 individuals per species at each concentration level were counted with a micrometer fitted to a compound microscope. To minimize sampling errors, spheres were counted only from animals with full guts. Elimination of individuals with unfilled guts required pooling data from the replicated treatments. Data was recorded as the number of spheres of each size per individual of each species.

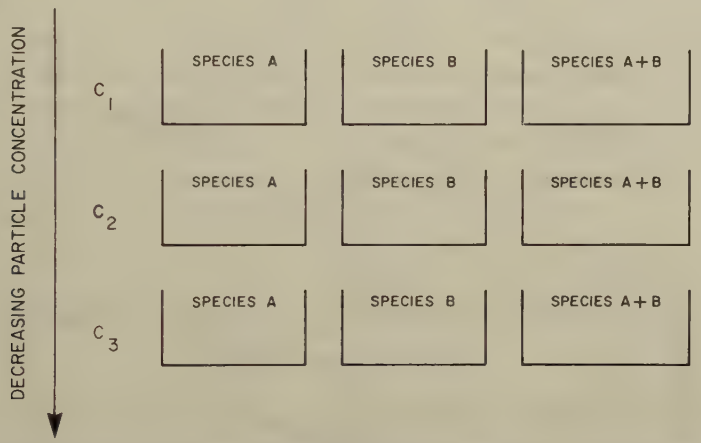

Fig. 1. The experimental design of the resource partitioning experiments: the abundance of C_1 is twice that of C_2 and four times that of C_3.

The experiments were conducted during October, 1976, February, 1977, March, 1977, and June, 1977. For the first three dates two species were used and for the June experiment all three species were used. The seasonal availability of copepods determined which species were used for each experiment. *Acartia hudsonica* and *Temora longicornis* were used during October, *Pseudocalanus* sp. and *Temora longicornis* in February, *Acartia hudsonica* and *Pseudocalanus* sp. during March, and all three species in June.

The method of Roughgarden (1974) was used to evaluate the resource utilization data. The population resource utilization function, H_x, is the probability that a unit of the population's food requirements will come from size x on the resource axis (Fig. 2). Let $\rho(x|y)$ denote the probability that an individual of phenotype y

will take resources from position x (Roughgarden, 1972). Phenotype is defined as cephalothorax length with the various phenotypes differing by 0.1 mm in length. By the rules of conditional probability, H_x is apportioned among phenotypes as,

$$H_x = \sum_y P(y)\ \rho(x|y), \tag{1}$$

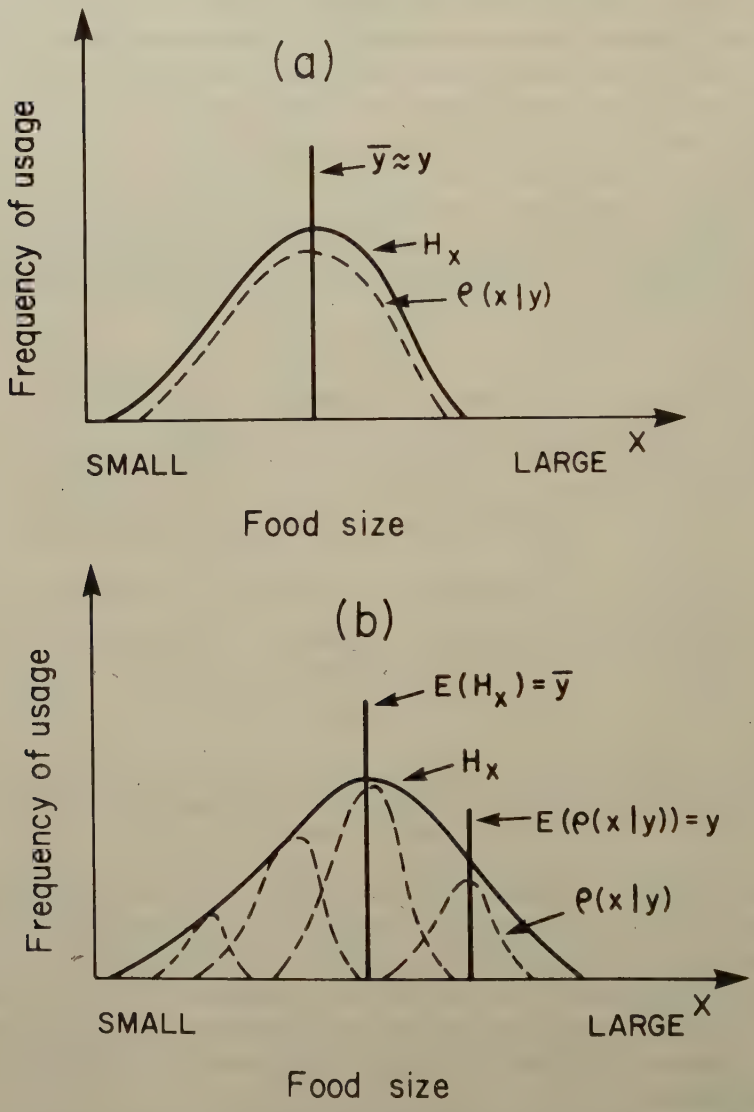

Fig. 2. H_x is the population resource utilization function: $\rho(x|y)$ is the resource utilization function of a phenotype; $\bar{y}$ is the average food size ingested by the population; the average food size ingested by a particular phenotype is y; (a) each phenotype has approximately the same resource utilization function as the population; (b) each phenotype has a different utilization function from that of the population; note that y and $\bar{y}$ differ from the notation in the text, but the interpretation is clear.

where $P(y)$ is the distribution of phenotypes in the population. Thus, the total niche width (TNW) is measured by the variance of the population resource utilization function, H_x and is denoted by $\mathrm{Var}(H_x)$ so,

$$\mathrm{Var}(H_x) = \mathrm{WPC} + \mathrm{BPC} = \sum_y P(y)\ \mathrm{Var}(\rho(x|y) + \mathrm{Var}(P(y)), \tag{2}$$

where WPC is the within phenotype component and BPC is the between phenotype component of the total niche width. Each phenotype is equated with the average ingested sphere size such that the between phenotype component (BPC) measures the deviation of each phenotype's average food size usage from the average of the population.

Two phenomena are represented in the composition of a population's total niche width. The first is that each phenotype displays variation in its resource usage (WPC). Secondly, there is variation among phenotypes in resource use (BPC). The WPC is a measure of intraphenotypic competition, while the BPC measures interphenotypic competition. In other words, when the BPC is very close to zero, the niche width for each phenotype is similar to that for the entire population. When the BPC is larger than zero, phenotypes correspond to distinct niche widths (i.e. the population is defined as polymorphic). So far the analysis assumes that each phenotype uses the same amount of the resource regardless of the position of the resource on the food size axis. This assumption is not justified, and a weighting function must be introduced. Let $a(y)$ be the amount of resource used by a phenotype at location x on the resource axis. The average amount consumed, $\bar{a}$, is then

$$\bar{a} = \sum_y P(y)\ a(y). \tag{3}$$

The weighted frequency distribution of the phenotype averages, $P'(y)$, is

$$P'(y) = (a(y)/\bar{a})P(y). \tag{4}$$

$P'(y)$ is then substituted for $P(y)$ in Equation (1) to account for differences in resource consumption.

Differences among niche widths over seasonal gradients of food concentration were tested for statistical significance by the F-test.

Results

These experiments measured (1) the seasonal patterns of sphere usage of each species in the absence and presence of another species; (2) seasonal change in the total niche width and the between phenotype component of niche width for each species; and (3) seasonal changes in the quantities of spheres ingested in the presence and absence of other species.

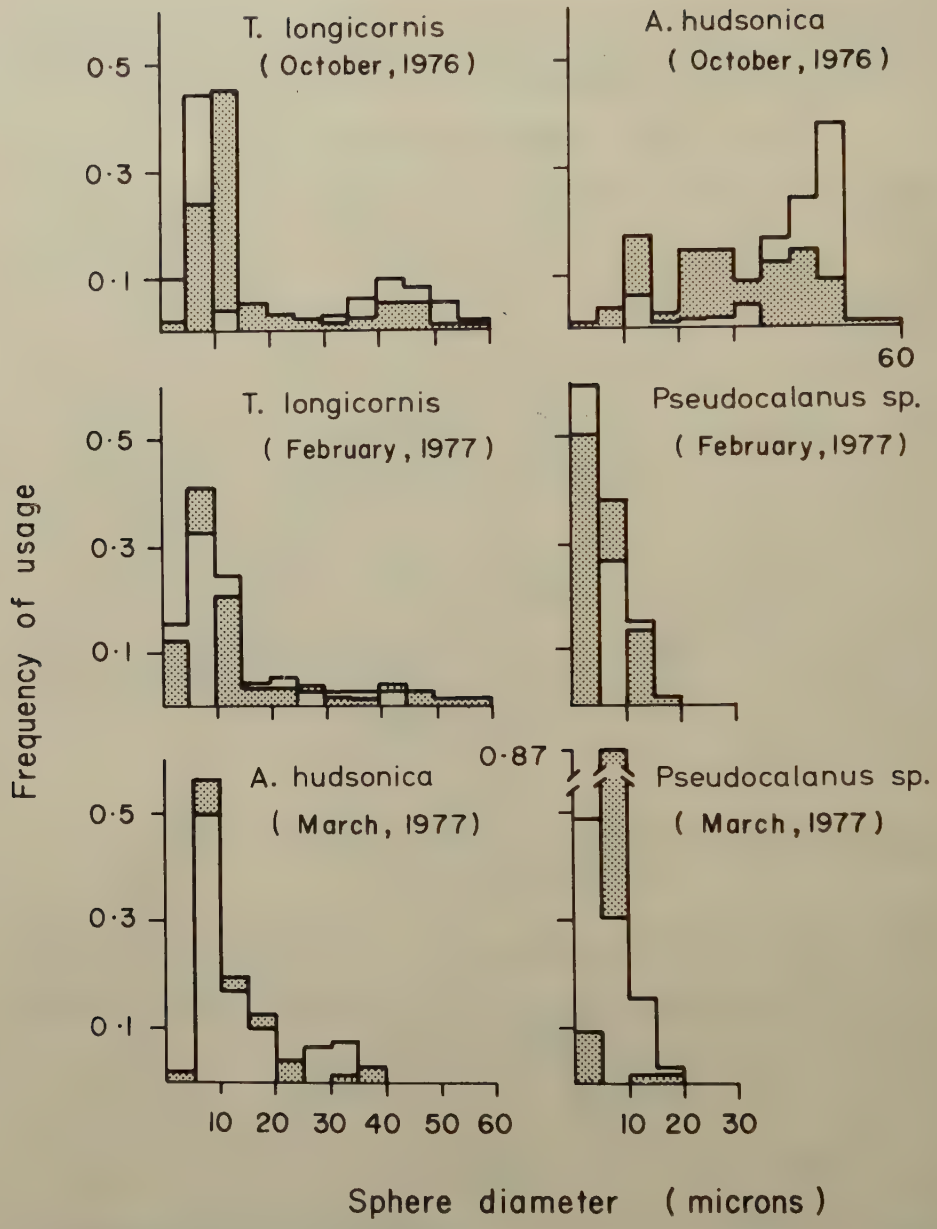

Fig. 3. The seasonal resource utilization distributions: stippled histogram is a species food size usage in the presence of another species; unstippled histogram is the same species food size usage in the absence of another species; each species histogram was constructed from spheres in the guts of at least 90 individuals.

SEASONAL RESOURCE UTILIZATION

The variance of the resource usage distributions of *Temora longicornis* decreased from October to June (Figs. 3, 4). Resource usage in the presence and absence of other species by *T. longicornis* shifted significantly ($\chi^2 = 434.2$, $P < 0.001$) in the presence of *Acartia hudsonica* in October but did not differ significantly in the presence of other species during the other seasons (Figs. 3, 4).

The variance of the resource utilization distributions for *A. hudsonica* decreased from October to June both in the absence and presence of other species (Figs. 3, 4). For *A. hudsonica* resource usage did not change in the presence of *Pseudocalanus* sp. in March or in the presence of *Temora longicornis* in June; the largest shifts in resource were associated with *T. longicornis* ($\chi^2 = 198.4$, $P < 0.001$) in October and with *Pseudocalanus* sp. ($\chi^2 = 160.8$, $P < 0.001$) in June (Figs. 3, 4).

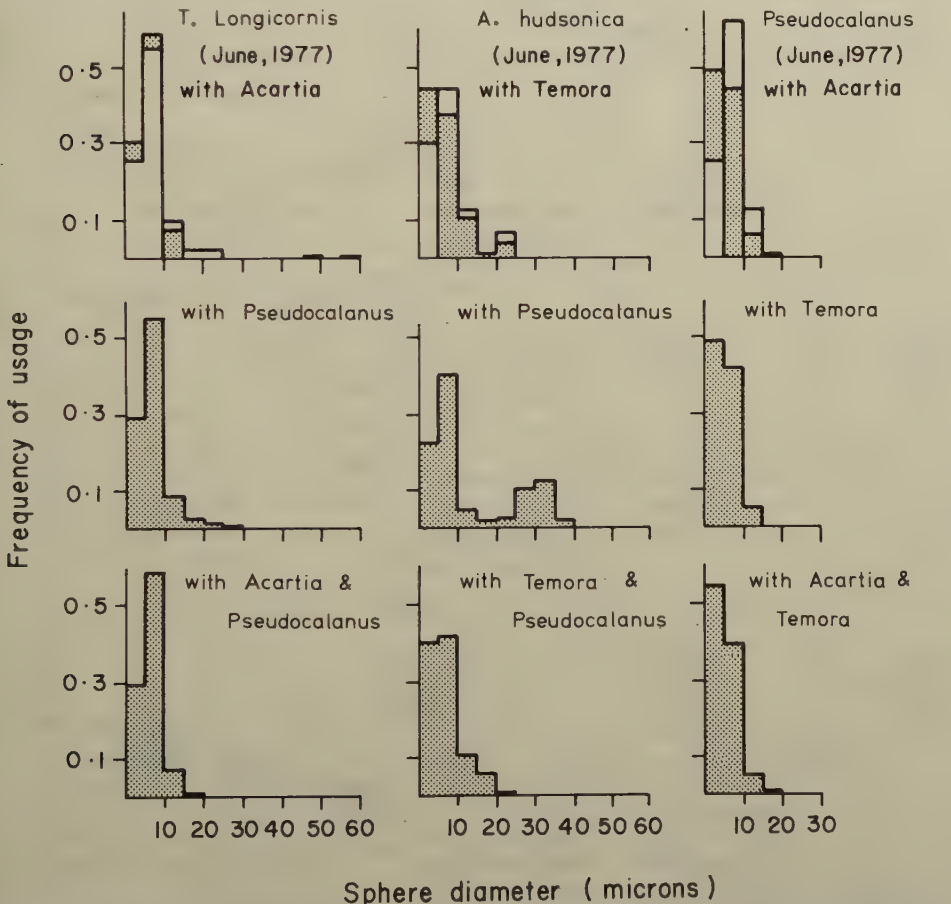

Fig. 4. The resource utilization distributions of each species alone (unstippled) and in the presence of one and two other species (stippled): each species histogram was constructed from the spheres in the guts of at least 90 individuals.

The resource usage patterns of *Pseudocalanus* sp. remained relatively constant in the absence of other species for each season (Figs. 3, 4). There was no significant difference ($\chi^2 = 8.4$, $P > 0.05$) in resource usage in the presence of *Temora longicornis* in February, but in March ($\chi^2 = 144.7$, $P < 0.001$) and June ($\chi^2 = 30$, $P < 0.01$) resource usage changed in the presence of other species.

The TNW of *T. longicornis* decreased significantly (F-test, $P < 0.05$) from October to June; the % BPC remained relatively constant over all seasons (Fig. 5). The TNW and % BPC of *Acartia hudsonica* decreased significantly (F-test, $P < 0.001$) from

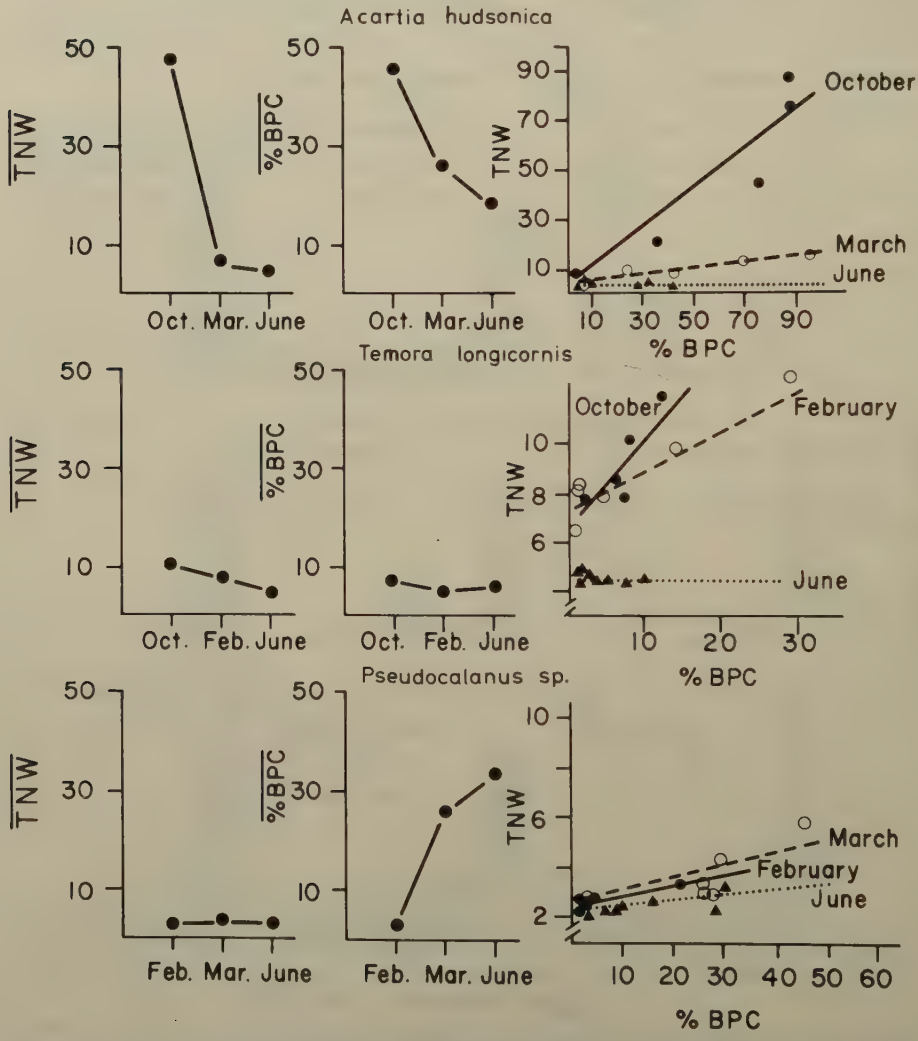

Fig. 5. The seasonal behaviour of $\overline{\text{TNW}}$ and % $\overline{\text{BPC}}$: $\overline{\text{TNW}}$ and % $\overline{\text{BPC}}$ are the TNW and % BPC averaged over the seasonal gradient of food abundance.

October to June (Fig. 5). For *Pseudocalanus* sp. the TNW remained constant; the % BPC increased (F-test, $P < 0.001$) from October to June (Fig. 5).

The dependence of the TNW on the % BPC decreased seasonally so that in June differential phenotypic resource specialization did not increase niche width. The sensitivity of the TNW to the % BPC was greater for *Acartia hudsonica* than for *Temora longicornis*. That TNW did not increase with % BPC in June for each species suggests that interphenotypic competition was keen. The seasonal change of TNW was not correlated with seasonal change in cephalothorax length.

The proportion of individuals of *T. longicornis* and *Acartia hudsonica* ingesting spheres >30 μm decreased from October to June (Fig. 6) demonstrating that the seasonal decrease in TNW was related to the percentage of bimodal feeders. Both of those species have unimodal (ingestion of spheres <30 μm) as well as bimodal (ingestion of spheres both <30 μm and >30 μm) feeders. There was no relationship between an individual's mode of feeding and body length. The seasonal decrease in bimodal feeders suggests that individual copepods are tracking some property of the food environment.

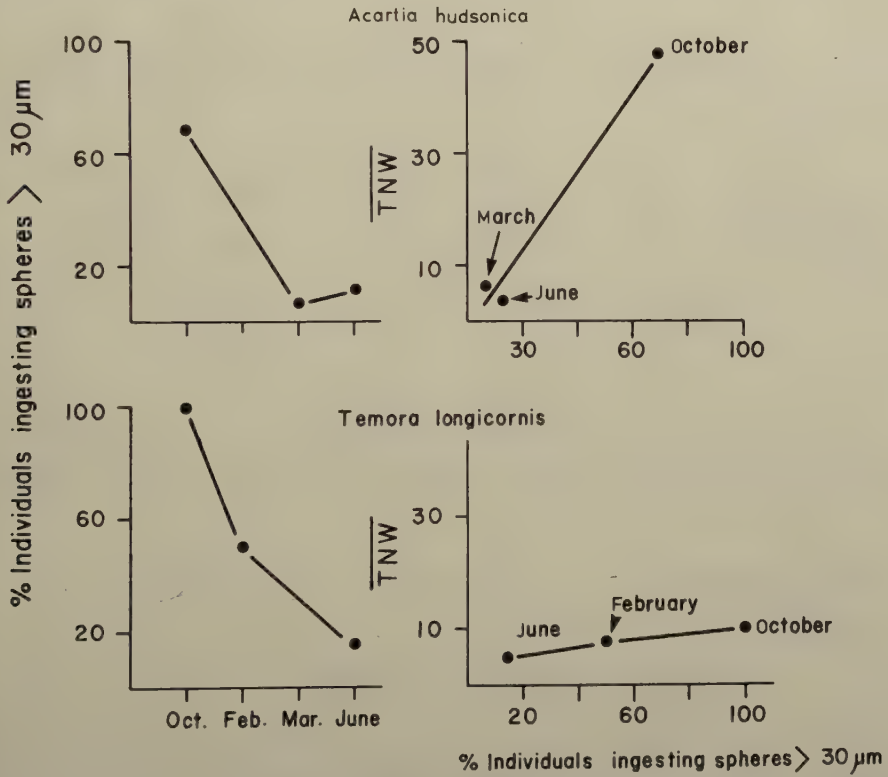

Fig. 6. The seasonal decrease of the percentage of individuals ingesting spheres >30 μm: $\overline{TNW}$ is the total niche width averaged over the gradient of food abundance; *Pseudocalanus* sp. never ingested spheres larger than 30 μm.

SEASONAL QUANTITIES OF SPHERES INGESTED IN THE PRESENCE AND ABSENCE OF ANOTHER SPECIES

A large seasonal decrease in average volume ingested/copepod ($\mu m^3 \times 10^3$) of *Temora longicornis* was seen in the absence and presence of other species (Fig. 7). Volumes ingested were significantly less (*t*-test, $P < 0.005$) in the presence of another species, with the exception of *Pseudocalanus* sp. during March.

The average volume ingested/copepod by *Acartia hudsonica* decreased seasonally both in the presence and absence of other species (Fig. 7). Volumes ingested were significantly different (*t*-test, $P < 0.005$) in the presence of other species with the exception of *Pseudocalanus* sp. during June.

The average volume ingested/copepod by *Pseudocalanus* sp. decreased from February to March but increased during June (Fig. 7). In the presence of other species the average volume ingested/copepod was significantly greater (*t*-test, $P < 0.005$), except in the presence of *Acartia hudsonica* during June. The average volume ingested/copepod was largest for *Temora longicornis* and smallest for *Pseudocalanus* sp.

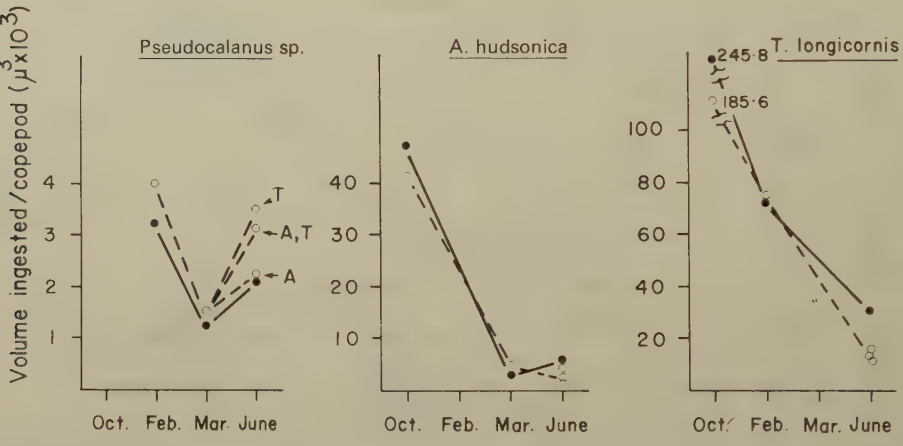

Fig. 7. Volume of spheres ingested by each species in the absence (●) and in the presence (○) of other species.

SINGLE SPECIES RESPONSE OVER A GRADIENT OF FOOD CONCENTRATION

These results catalogue the food-size preferences of each species over a gradient of food concentration as measured by TNW and BPC. The TNW of *Temora longicornis* did not increase or decrease significantly (*F*-test, $P > 0.05$) in October or February but increased (*F*-test, $P < 0.05$) in June while the % BPC increased (*F*-test, $P > 0.01$) in each season as particle concentration decreased (Fig. 8). The TNW over a food gradient of *Acartia hudsonica* increased significantly in October (*F*-test, $P < 0.001$), but decreased (*F*-test, $P < 0.01$) in March and June. % BPC increased

(F-test, $P < 0.01$) in October and June, but decreased (F-test, $P < 0.01$) in March (Fig. 9). In contrast, the TNW of *Pseudocalanus* sp. did not change (F-test, $P > 0.05$) over the gradient in any season (see Fig. 10).

As food levels decreased each species became polymorphic in its food usage, indicating that the degree of overlap of resource usage among the various phenotypes decreased. TNW increased over the gradient, although the increase was not significant. The magnitude of change of TNW and % BPC for *Acartia hudsonica* suggests that this species may be very sensitive to both food variability and abundance.

MIXED SPECIES RESPONSES OVER A GRADIENT OF FOOD CONCENTRATIONS

In October, neither the TNW nor % BPC of *Temora longicornis* were significantly different (F-test, $P > 0.05$) in the presence of *Acartia hudsonica*. While in February

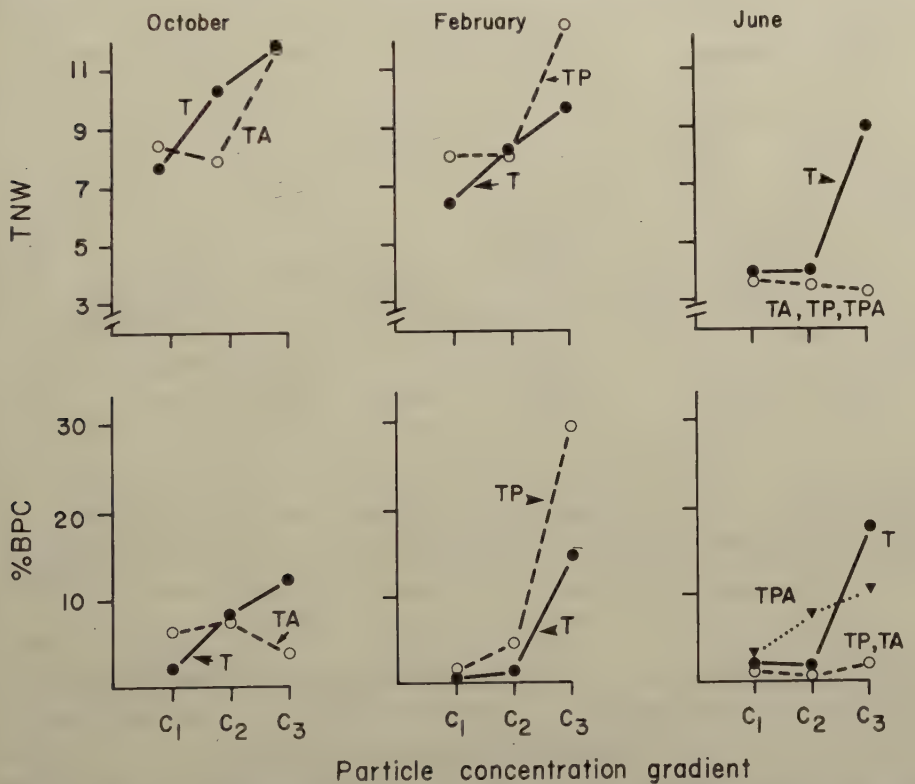

Fig. 8. The TNW and % BPC of *Temora longicornis* over a gradient of food abundance in the presence and absence of other species: % BPC is the percent between phenotype component of niche width; TNW is the total niche width; T is *T. longicornis* in the absence of other species; TA is *T. longicornis* in the presence of *A. hudsonica;* TP is *T. longicornis* in the presence of *Pseudocalanus* sp., TPA is *T. longicornis* in the presence of *A. hudsonica* and *Pseudocalanus* sp.; the abundance of C_1 is twice that of C_2 and four times that of C_3.

the % BPC increased (F-test, $P < 0.01$) in the presence of *Pseudocalanus* sp. but the TNW did not. In June the TNW was not significantly changed (F-test, $P > 0.05$) by any species combination. The % BPC decreased (F-test, $P < 0.01$) in the presence of either *Acartia hudsonica* or *Pseudocalanus* sp. but did not change significantly (F-test, $P > 0.05$) with both species present (Fig. 8).

The TNW and % BPC of *Acartia hudsonica* decreased significantly (F-test, $P < 0.001$) in the presence of *Temora longicornis* in October. In March and in June the TNW and % BPC increased (F-test, $P < 0.05$) in the presence of *Pseudocalanus* sp. In the presence of *Temora longicornis* the TNW did not change significantly (F-test, $P < 0.05$) although the BPC decreased (F-test, $P < 0.001$). Neither the TNC nor % BPC changed significantly when both species were present (Fig. 9).

For *Pseudocalanus* sp. in February, the TNW did not change significantly, but the % BPC decreased when *Temora longicornis* (F-test, $P < 0.001$) was present. During

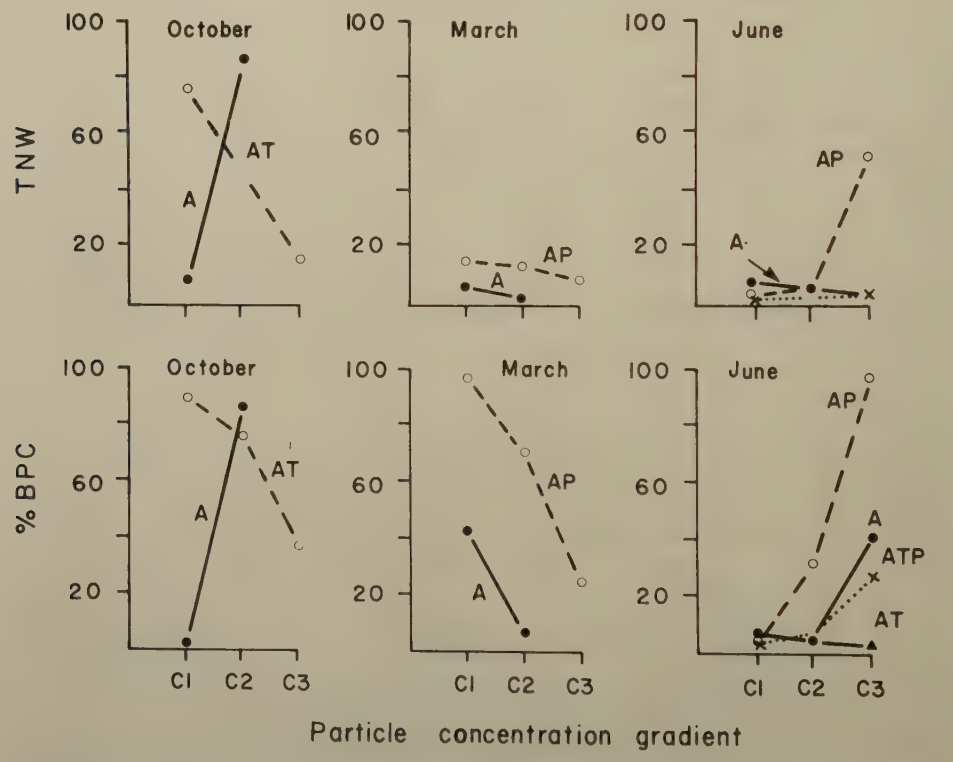

Fig. 9. The TNW and % BPC of *Acartia hudsonica* over a gradient of food abundance in the presence and absence of other species: TNW and % BPC are the total niche width and percent between component of the total niche width; A is *A. hudsonica* in the absence of other species; AP is *A. hudsonica* in the presence of *Pseudocalanus* sp.; AT is *A. hudsonica* in the presence of *T. longicornis*; ATP is *A. hudsonica* in the presence of *T. longicornis* and *Pseudocalanus* sp.; the abundance of C_1 is twice that of C_2 and four times that of C_3.

March, neither the TNW nor the BPC of *Pseudocalanus* sp. changed significantly in the presence of *Acartia hudsonica*. In June the TNW did not change, but the % BPC decreased significantly for all combinations of *Pseudocalanus* sp. (F-test, $P < 0.01$) with other species (Fig. 10).

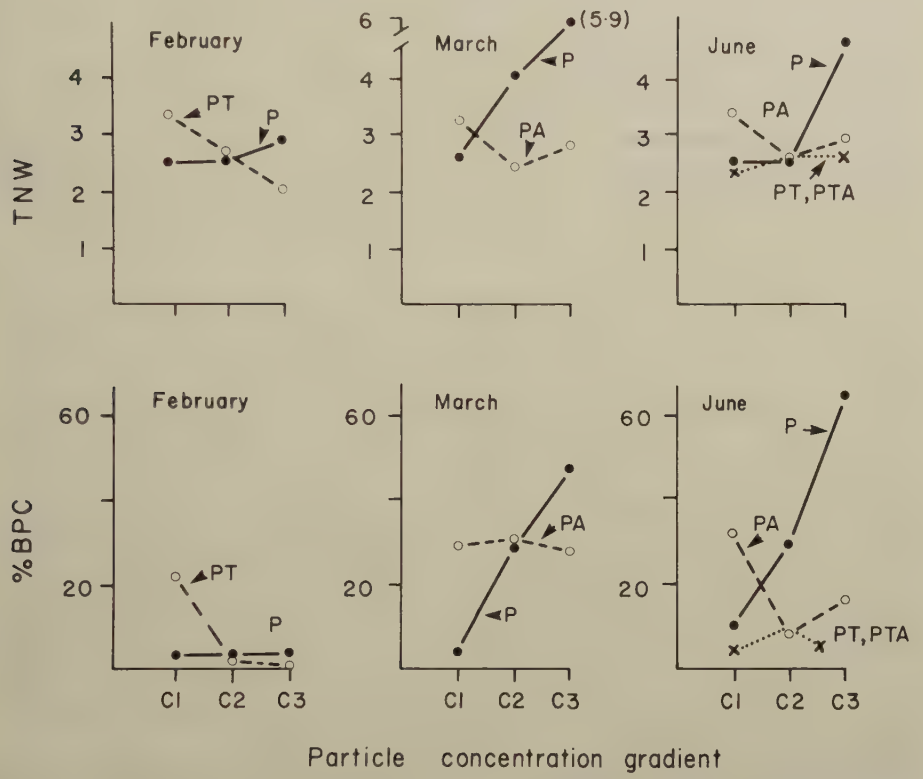

Fig. 10. *Pseudocalanus* sp.: TNW is the total niche width; % BPC is the percent between phenotype component of niche width; P is *Pseudocalanus* sp. in the absence of other species; PA is *Pseudocalanus* sp. in the presence of *Acartia hudsonica*; PT is *Pseudocalanus* sp. in the presence of *Temora longicornis*; PTA is *Pseudocalanus* sp. in the presence of *Acartia hudsonica* and *Temora longicornis*.

Species specific TNW and/or % BPC changed over a food concentration gradient when another species was present. The direction and magnitude of the change depended upon both season and species combination. The results do not imply competitive interactions, but clearly they do show that copepods respond to their food environment differently in the presence of another species.

Discussion

Resource partitioning patterns

Predictions of the relationships and interaction among coexisting species that use a common limiting resource have been developed primarily from the theoretical work of MacArthur & Levins (1967) and MacArthur (1972). Most empirical investigations of resource partitioning have dealt with relationships among species for which the limiting resources were not well defined (for an exception, see Pulliam, 1974). Useful notions of habitat and niche relationships among coexisting species, however, have been derived from empirical studies of resource partitioning (e.g. Schoener, 1974). In the present study, empirical descriptions of resource partitioning patterns suggest some basic principles influencing the food partitioning patterns of coastal marine copepods.

A minimum of two resource dimensions is involved in the partitioning patterns of these species. The seasonal vertical migration patterns of *Acartia hudsonica*, *Pseudocalanus* sp. and *Temora longicornis* have been documented by Atherton (pers. comm.). *Acartia hudsonica*, which has the smallest annual amplitude of migration has the highest annual food niche width. *Pseudocalanus* sp. has the greatest amplitude of migration and the smallest food niche width. *Temora longicornis*, on the other hand, has an annual food niche width and amplitude of migration that are between those of the other two species. Apparently food niche width is inversely related to amplitude of vertical migration. This is consistent with observations by Cody (1974) who has documented the general tendency for habitat generalists to be food specialists and habitat specialists to be food generalists for several species of birds. Amplitude of vertical migration is a poor estimator of habitat usage; measures such as the proportion of time spent in a particular patch or proportion of time spent at a particular stratum may be a better index.

The spatial–temporal variability of phytoplankton species composition and abundance is high in the Bedford Basin system (Platt, 1975), so that individual copepods will probably encounter a wide range of food sizes, types, and abundance. There is a consistent seasonal shift from a large proportion of dinoflagellates in October to large proportions of diatoms in March and small flagellates in June. The mean and variance of dinoflagellate cell sizes decreases from October to June, while for diatoms these measures increase over the same time period (Fig. 11). These seasonal differences in the particle spectra suggest that the seasonal decrease in total niche width exhibited by *Acartia hudsonica* and *Temora longicornis* may be related to (1) a seasonal decrease in the mean dinoflagellate cell size, and (2) a seasonal decrease in the variance of dinoflagellate cell sizes. This is supported indirectly by the fact that the carbon content of many dinoflagellates is considerably higher than that of diatoms of the same or larger size (Paffenhofer, 1976), and that the cellulase levels of *T. longicornis* and *Acartia hudsonica* in the Bedford Basin

are highest in October and lowest in June (Mayzaud & Conover, 1975). These reports together with the seasonal decrease of the niche widths of *A. hudsonica* and *Temora longicornis* suggest that these copepods track the seasonal dinoflagellate variability. Furthermore, the observed overlap in seasonal increase of sphere size for the same two species suggests that the degree of food resource partitioning is related to temporal variability in dinoflagellate cell size. The seasonal TNW shift exhibited by *Acartia hudsonica* and *Temora longicornis* may be related to properties of the particle spectrum other than variability of dinoflagellate cell size or to overlap of different copepod generations. This seasonal shift is striking in comparison to the constant seasonal niche width of *Pseudocalanus* sp. One is tempted to speculate that the feeding pattern of *Pseudocalanus* sp. may be a consequence of some simple anticipatory mechanism.

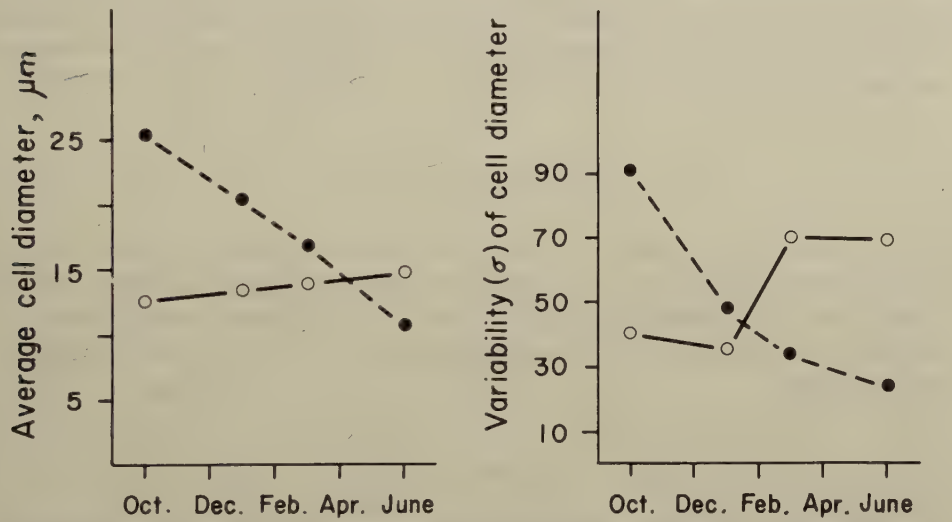

Fig. 11. Comparison of the seasonal mean and standard deviation (σ) of diatom and dinoflagellate cell diameter in the Bedford Basin: ○, diatoms; ●, dinoflagellates (P. A. Lane, unpubl. data).

Interspecific interactions often altered total niche width and the between phenotype component of niche width although the magnitude and direction of change was dependent upon season. Strongly asymmetric interactions occurred between *Pseudocalanus* sp. and *Acartia hudsonica* even when their niche widths differed markedly, suggesting that interference mechanisms such as microscale hydrodynamic disturbance (Strickler, pers. comm.) may be important in structuring food partitioning patterns. The high phytoplankton productivity in the Bedford Basin and the seasonality of the food environment may minimize competitive "bottlenecks" so that the size selective predation by invertebrate and vertebrate predators may have a stronger influence upon food partitioning patterns.

The tendency for total niche width to increase as food levels decrease has also been found for marine copepods (Cowles, 1977) in the Peru upwelling system, for birds (Lack & Owen, 1955), and for gastropods of the genus *Conus* (Kohn, 1968). These results correspond to the most general prediction of optimal foraging theory – that the breadth of food types will increase and the diet becomes less specialized as food abundance decreases (MacArthur & Pianka, 1966; Emlen, 1968; Schoener, 1971; Pulliam, 1974). While no direct evidence is available that copepods exhibit optimal foraging the results of this study indicate that some copepods modify their mechanisms of food capture as food abundance changes.

It has been shown here that both species interactions and the seasonal variance in the particle size spectra influence copepod feeding patterns. It is not clear, however, that dinoflagellates including the genus *Ceratium*, are an important food source for *Acartia hudsonica* and *Temora longicornis* even though their niche widths are positively correlated with dinoflagellate cell size variability. Future work is needed on the nature of the species interactions, the rôle of dinoflagellates as a food source, and particularly the rôle of food variation within and between copepod generations.

Acknowledgements

This research was supported by National Research Council of Canada grant (9222-203-025) to Dr. P.A. Lane and Dalhousie University graduate awards. I thank Drs. M. Brylinski, R. Doyle, P. Lane and I. McLaren for advice and suggestions. Many thanks to Dr. R. Conover and Jennifer Cassells for critically reading the manuscript.

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J. exp. mar. Biol. Ecol., 1980, Vol. 44, pp. 247–251
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THE EFFECT OF EARLY STARVATION ON LATER FEEDING SUCCESS OF KING CRAB ZOEAE[1]

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Abstract: First zoeae of Cook Inlet king crab, *Paralithodes camtschatica* (Tilesius), were held at 2, 4, and 6 °C and starved for 12, 60, and 84 h, then a known number of prey organisms were made available. Zoeae first fed at age 12 and 60 h were able to successfully capture prey. Zoeae starved for 84 h and held at 6 °C retained the ability to capture prey; however, there was a significant reduction in predation rates in comparison to zoeae starved for shorter periods and held at this temperature. The zoeae starved for 84 h and held at 2 and 4 °C were generally unable to capture prey.

The results of the study indicate that prey availability when the zoeae first begin to feed has more effect on later feeding success than water temperature. King crab zoeae that receive food within 60 h of hatching are capable of capturing prey thereafter if prey concentrations are adequate. If feeding is delayed an additional 24 h, the ability to capture prey is reduced, especially at water temperatures <4 °C.

INTRODUCTION

Marked variations in year class abundance of many species of commercially harvested crabs occur, but the reasons for these fluctuations are generally unknown. The planktonic larval stage is the period in their life history when most species of crab are subjected to the highest mortality rates (Warner, 1967). Differential annual mortality of planktonic larvae is one hypothesis proposed to explain variations in the size of year classes of many organisms (Hjort, 1926).

Probably several physical and environmental factors interact to affect mortality rates of king crab larvae; among them, temperature, stormy conditions, and prey availability have been identified (Ishimaru, 1936; Satoe, 1958; Paul *et al.*, 1979). Several laboratory studies have demonstrated that prey concentrations must be high, 600 to 1600 organisms of suitable size per liter, to obtain moderate survival rates of crab zoeae in captivity (Brick, 1974; Bigford, 1978). Paul *et al.* (in press) determined that prey population densities have to be of the order of 40 to 80 per liter for king crab zoeae to successfully capture prey.

Recent work has demonstrated extensive mortality in some species of larval fishes when there is a lack of food of a proper size and nutritional value during the period when the first begin to feed (see review of Hunter, 1976). A similar "critical" period

[1] Contribution number 393 from the Institute of Marine Science, University of Alaska.

probably exists for decapod larvae. Modin & Cox (1967) found that if zoeae of the shrimp *Pandalus jordani* were not fed soon after hatching, survival rates were low irregardless of prey concentrations at a later time. Kon (1979) observed that if the zoeae of *Chionoecetes opilio* were starved for more than 3 days a significant decline in molting success occurred. The length of time the first zoeae of *Paralithodes camtschatica* (Tilesius) can be starved before their vitality is affected is not documented. The objective of this study is to describe the effect of starvation for controlled periods on the later ability of king crab first zoeae to feed.

Materials and Methods

A female king crab with hatching eggs captured in Cook Inlet, Alaska, was placed in a tank with static water at 1700. Temperature was kept at 5 °C. Stage 1 zoeae were removed for experiments the following morning at 0800 and hatching time was assumed to be 0000. Zoeae were placed in beakers (125 mm high, 90 mm diameter) containing 500 ml filtered sea water, salinity 33‰, and concentrations of five zoeae per beaker. The outside of each beaker was covered with black plastic and a light source of 350 lux maintained directly overhead 24 h a day. The temperature in three beakers was maintained at 2 °C (SD = 0.0 °C), while two similar sets of three beakers each were held at 4 °C (SD = 0.0 °C) and 6 °C (SD = 0.8 °C), respectively. The zoeae in one beaker of each temperature group, age assumed to be 12 h, received food immediately and every 24 h thereafter. The zoeae in the second and third beakers of the three temperature groups were first fed after 60 h and 84 h of starvation, respectively.

The prey consisted of wild copepods and copepodids, primarily of the genera *Pseudocalanus*, *Acartia*, and *Oithona*, that passed through a 0.5-mm^2 screen but were retained by a 0.35-mm^2 screen. The average total length of prey organisms was 0.8 mm with a standard deviation of 0.1 mm. This size and type of prey was utilized because it proved successful in an earlier feeding study involving king crab zoeae (Paul *et al.*, 1979). Feeding was accomplished by placing the zoeae in beakers containing 50 prey organisms (prey concentration = 100 per liter). Thereafter, each day zoeae were moved to new beakers with 50 fresh prey.

A gentle flow of air which passed through an air stone at the bottom of each beaker was utilized to keep prey randomly dispersed and to prevent them from settling. The air flow was adjusted so that it did not interfere with the swimming of the zoeae.

Predation rates were determined by counting the number of prey remaining after 24 h of feeding. Three control beakers containing prey but no predators were used to check the accuracy of the counting method. All prey in control beakers were accounted for during the recount. All enumeration of prey was done with a dissection microscope. Feeding observations were continued for 7 days. Regression analysis (Snedecor, 1956) was used to examine the relationship between the number of hours

starved before feeding and the number of prey killed. The data used in the analysis includes all daily feeding observations for all three temperature groups. The validity of the correlation coefficient (r) was measured using the formula $t = \sqrt{vr^2/(1 - r^2)}$ where $v = n - 2$. The numbers, means, standard deviations, and standard errors of the mean of prey killed are illustrated in Fig. 1.

Results

The zoeae held at 2 °C and fed first at age 12 h killed a daily average of 3.8 prey organisms per zoea. Zoeae fed at the same age but held at 4 and 6 °C exhibited similar rates of predation, consuming an average of 3.7 and 4.4 prey per day (Fig. 1). The temperature of the water in the beakers apparently caused little difference in predation rates of zoeae fed at age 12 h (Fig. 1).

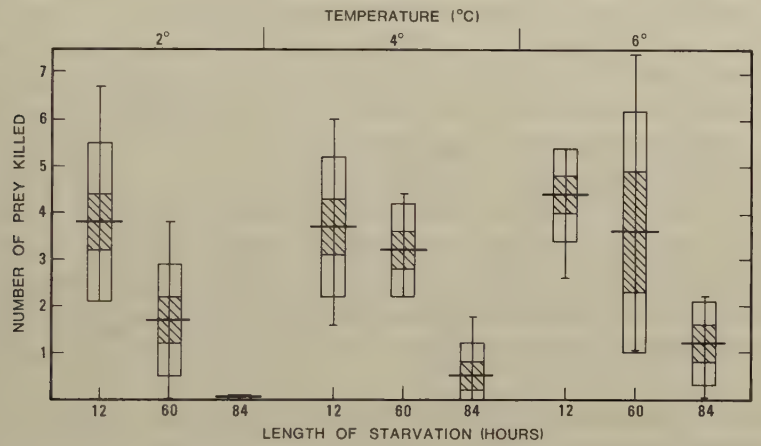

Fig. 1. The number of copepods killed by *Paralithodes camtschatica* Stage 1 zoeae starved for 12, 60, and 84 h and held at 2, 4, and 6 °C: shaded area, 2 SE of the mean; clear area, 2 SD of the mean; vertical line, range; horizontal line, mean.

The predation rate of the zoeae first fed at age 60 h and held at 2 °C was considerably lower, 1.7 prey per day, than that of their cohorts fed at age 12 h and zoeae in the other temperature groups fed at age 60 h (Fig. 1). The predation rates of zoeae first fed at age 60 h and kept at 4 and 6 °C and their cohorts held at the same temperature and fed at age 12 h were similar (Fig. 1).

The zoeae starved for 84 h, and kept at 2 and 4 °C were generally unable to capture prey; they consumed an average of 0.03 and 0.50 organisms per day respectively (Fig. 1). Zoeae starved for 84 h and held at 6 °C remained able to capture prey. However, their predation rate of 1.2 copepods per day was only one-third that of zoeae starved for 60 h and also held at 6 °C (Fig. 1).

The correlation coefficient, -0.860, indicates a high negative correlation between the number of hours starved and subsequent ability to capture prey. The t-distribution ($P = 0.95$) was found to be significant.

Discussion

In Cook Inlet, king crab eggs generally hatch from March through June (A. Davis, Alaska Dept. Fish and Game, Homer, Alaska, pers. comm.). During this period monthly mean sea-water temperatures are likely to range from 2 to 8 °C (U.S. Dept. Commerce, 1970). Therefore, it is probable that Cook Inlet king crab zoeae must forage for food during periods when the water temperatures fall within the range of 2 to 6 °C, used in this study. The lack of a substantial difference in the predation rate of Stage 1 zoeae fed at age 12 h and kept at 2, 4, and 6 °C (Fig. 1) indicates that prey availability when the zoeae first begin to feed is more important in determining feeding success than the sea-water temperature.

Paralithodes camtschatica exists as a Stage 1 zoea for ≈ 7 to 24 days depending on water temperature (Satoe, 1958). Including its four other larval stages, king crab larvae remain planktonic for 47 to 84 days (Satoe, 1958). Little is known about the feeding habits of larvae during this planktonic period. In the laboratory, king crab zoeae require prey concentrations of 40 to 80 per liter to feed successfully (Paul *et al.*, in press). If prey concentrations are sufficient, they will consume 12 copepods (Paul *et al.*, in press) or 25 *Artemia salina* nauplii per day (Nakanishi, 1976). Ishimaru (1936) reported reduced survival in year classes of king crabs subjected to predominantly stormy conditions during the planktonic larval period. It is possible that mixing due to storms interferes with the feeding success of these active zoeae.

The results of this study indicate that if the first-stage zoeae of king crabs from Cook Inlet receive food within 60 h of hatching, they are capable of capturing prey thereafter if prey organisms are available at sufficient concentrations. If feeding is delayed an additional 24 h, their ability to feed will be impaired, especially if the water temperature is 4 °C or less, and their chances for survival will be reduced. The survival rate of *Chionoecetes opilio*, similar-sized zoeae found with king crab zoeae in nature, also declines if they are starved for the first 3 days of life (Kon, 1979).

Acknowledgements

This study was supported under Contract 03-5-022-56 between the University of Alaska and National Oceanographic and Atmospheric Administration, Department of Commerce, through the Outer Continental Shelf Environmental Assessment Program to which funds were provided by the Bureau of Land Management, Department of Interior. Facilities were provided by the Institute of Marine Science's

Seward Marine Station, University of Alaska. Nici Murawsky edited and typed this report. Dr. R. Lasker suggested many useful changes in the manuscript.

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J. exp. mar. Biol. Ecol., 1980, Vol. 44, pp. 253–260
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FEEDING EXPERIMENTS ON *PENILIA AVIROSTRIS* Dana (CLADOCERA: CRUSTACEA)

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Abstract: Feeding in the marine cladoceran, *Penilia avirostris* Dana, was investigated using plastic micronic beads as a controlled particle source. The range of bead size ingested by *P. avirostris* was largely limited to diameters of 20 μm and below, perhaps a competitive advantage in nature. It was found that: (1) as the concentration of beads increased, the number of beads ingested increased; (2) as the number of *P. avirostris* increased, the number of beads ingested increased; and (3) the number of beads ingested also increased with body size. The size of *P. avirostris*, however, did not appear to limit the size of bead ingested, while larger sized animals may be better competitors for particles.

INTRODUCTION

Feeding in *Penilia avirostris*, a marine cladoceran, was investigated by Lochhead (1936), who dealt with the use of appendages and the currents produced by them. The present study was designed to investigate whether there might be competition for different sizes and quantities of particles among the size classes of *P. avirostris* Dana, how superfluous particles or animals might cause a change in ingestion, and how different sizes of particles or animals might cause a change in ingestion.

MATERIALS AND METHODS

Plastic micronic beads were used as the source of particulate matter (Burns, 1968; Wilson, 1973). According to the manufacturers' specifications, the beads are of uniform size, shape, and consistency; they do not fracture easily, they can readily be seen in the gut of *P. avirostris*, and they are not chemically attractive or repellant. The size of beads used ranged nominally in diameter as follows: <1 to 20 μm, 20 to 30 μm, 30 to 40 μm, 40 to 50 μm, 60 to 70 μm, and 70 to 80 μm. These are the smallest sizes of micronic beads available. The range 50 to 60 μm is apparently not manufactured. In practice, there was some overlap between the size ranges.

Animals used in the experiments were collected from Kingston Harbour, Jamaica, close to the Port Royal Marine Laboratory, using 111.9 and 147.3 mesh per cm nylon nets. The sea temperature at the time of collection ranged between 25 and 27 °C. The body lengths (measured from the tip of the head to the end of the body) of *P. avirostris* collected varied between 500 and 1100 μm. In preparation for the

experiments, each grade of bead was washed three times in deionized distilled water and then in Millipore (0.45 μm) filtered sea water. Millipore filtered sea water was also used as the medium to ensure the absence of food material. The *P. avirostris* were placed in a darkened laboratory, and allowed to acclimate to a temperature of 20 °C for half an hour in filtered sea water. To maintain constant temperature conditions in the tropics requires air conditioning, and it is inevitable the laboratory temperatures will usually be a little lower than the prevailing sea temperature. The animals were then transferred to 140-ml bottles of filtered sea water, to which the bead suspension had been added from a measuring pipette. The bead concentration was measured by adding the beads to water, agitating the bottle, and counting the number of beads by use of a haemocytometer chamber. This was repeated for each bottle used in the experiment. The bottles containing beads and animals were then placed on a plankton wheel for 1 h. The plankton wheel consisted of a vertically mounted circular disc, 45 cm in diameter, on which bottles could be placed. The wheel was rotated at the rate of 3 r/min to keep the beads in suspension. The beads stayed in suspension throughout the experiments, no clumping of beads was observed in a bottle during an experiment. At the end of the experiment, the bottles were quickly removed from the wheel and the *P. avirostris* killed and preserved by adding a few drops of formalin to the medium. This method killed the animals quickly and without a loss of hindgut material.

The preserved animals were allowed to settle to the bottom of the bottles. Samples of 10 specimens per bottle were then removed and placed on a slide, and measurements taken of the beads in the guts. A microscope and ocular micrometer were used in measuring each *P. avirostris* in the subsample for body length, bead size, and number ingested. The subsample was returned to the original sample, and again allowed to settle out. The liquid was then siphoned off and the total number of *P. avirostris* per bottle counted.

Three series of experiments were conducted. (1) To determine the range of beads size ingested by *P. avirostris*. Each of the six size ranges was given separately to an average of 50 animals per bottle. The bead concentration was either (144 to 166) $\times 10^3$ or (72 to 84) $\times 10^3$ beads per ml. Each range of bead size and concentration was tested six times in repetitive experiments. (2) To examine the effect of bead concentration on the number of beads ingested by *P. avirostris*. The average number of animals per bottle was 165 to 175 in one experiment, and 460 to 475 in a second experiment. The concentration of beads per ml varied from (15 to 400) $\times 10^3$ and (80 to 320) $\times 10^3$, respectively; the experiments were run four and six times respectively. Approximately equal numbers of beads from each size range were used together for this and for Experiment (3). (3) To determine the effect of different concentrations of *P. avirostris* per bottle on the number of beads ingested. The bead concentration was (144 to 166) $\times 10^3$ beads per ml, while the concentration of *P. avirostris* was varied between 50 and 1300 per bottle. There were six replicates per experiment.

Results

In Fig. 1, the percentage of animals with ingested beads is shown for each size range of bead used. In the range of <1 to 20 μm beads, at a concentration of (144 to 166) $\times 10^3$ beads per ml, 60% of the animals ingested beads, while only 38% had ingested beads when the bead concentration was halved (shaded area). This general trend also appears for the ranges 20 to 30 μm, and 30 to 40 μm, while in the 40 to 50 μm range, both experiments gave the same low percentage. As each bead size range and bead concentration represents a separate experiment, the total percentage of all sections of the graph does not equal 100%. The size range of <1 to 20 μm beads appears to be ingested most frequently, and no beads >40 to 50 μm are ingested.

Scatter plots of the concentration of beads and the number of beads ingested per *P. avirostris* are shown in Fig. 2 for the two sets of experiments. In both experiments, the number of beads ingested per animal in a given time inreased with increasing

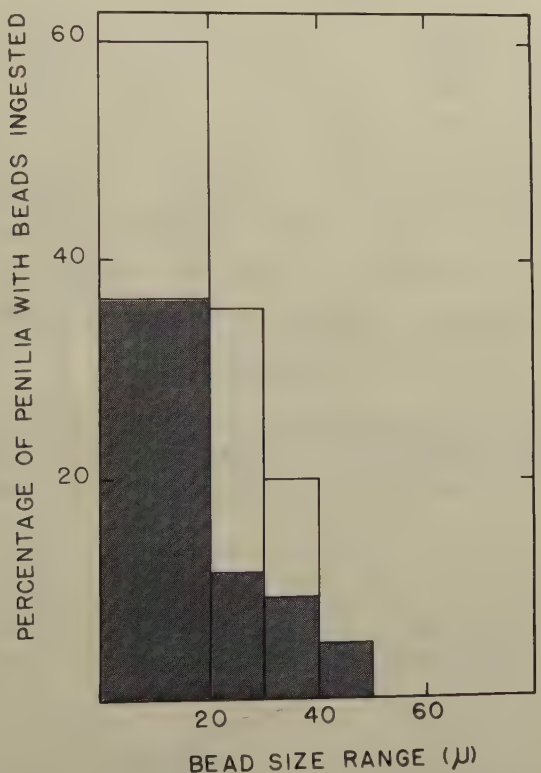

Fig. 1. Percentage of beads ingested by *Penilia* and the bead size per range: unshaded area, percentage ingested at a concentration of (144 to 166) $\times 10^3$ beads per ml; shaded area, percentage ingested at a concentration of (72 to 84) $\times 10^3$ beads per ml; the results for the two experiments in the 40 to 50 μm size range were the same.

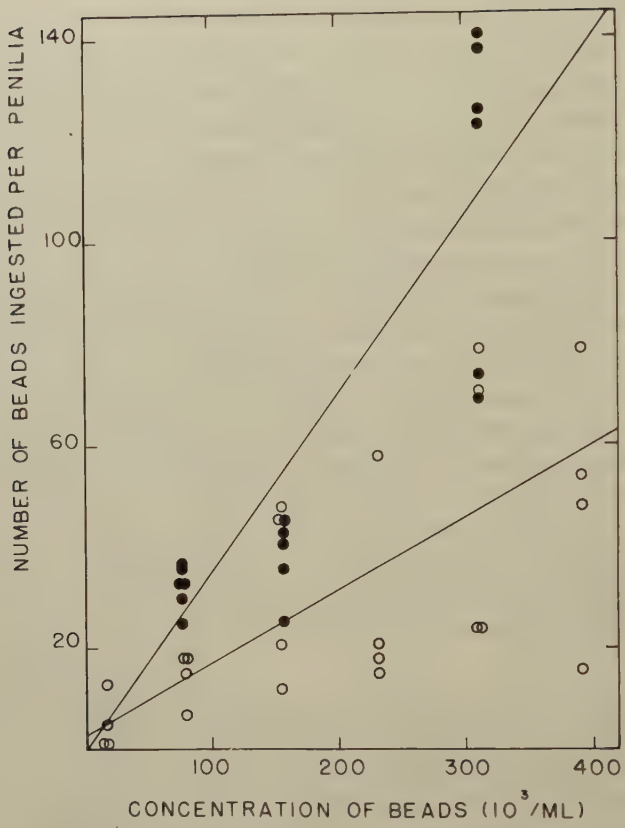

Fig. 2. Number of beads ingested per *Penilia* and the concentration of beads, using the complete bead size range: average number of *Penilia* per 140-ml bottle is 65 to 175 (○, lower curve), and 460 to 475 (●, upper curve).

concentrations of beads. The lines represent least-squares fits to the two sets of data and each has a P value of 0.001. The range of bead concentration has been given in the previous section. The uncertainty in counting the number of beads ingested is

TABLE I

Summary of experimental results.

Experimental variable	Ingestion of beads by *P. avirostris*	Cross correlation coefficient	P value	Significance
Increasing numbers of *P. avirostris*	Increased	0.633	0.001	Positive
Increasing bead concentration	Increased	0.844 (upper) 0.676 (lower)	0.001 0.001	Both positive
Increase in body length	Increased	0.964	0.001	Positive
Increase in bead size with body length	No increase or decrease	Median test (two-tailed)	>0.05	None

± 1 with practice. The larger numbers of *P. avirostris* (460 to 475) ingested more beads at a higher concentration than did the smaller numbers (165 to 175) of animals (Table I). As the concentration of *P. avirostris* increased, the number of beads ingested per animal also increased (Fig. 3). Of course, the bead concentration per animal decreased with increasing animal numbers (Table I). A least-squares line has been drawn through the points, with a P value of 0.001. The range of numbers of *P. avirostris* has been given in the previous section, and the uncertainty in

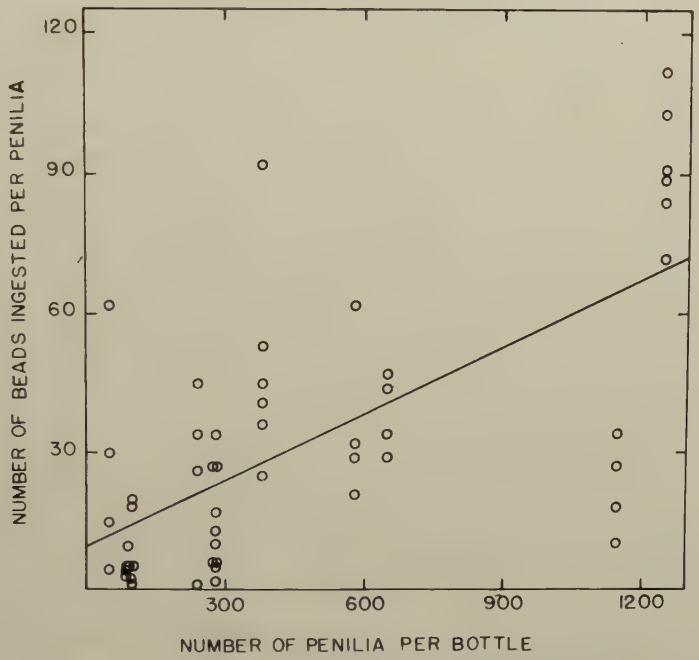

Fig. 3. Number of beads ingested per *Penilia* and concentration of *Penilia*: the initial bead concentration, using the complete bead size range, in each 140 ml bottle is (144 to 166) $\times 10^3$ beads per ml.

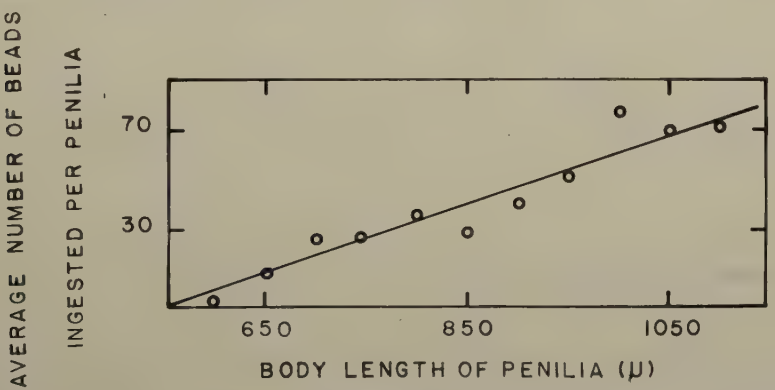

Fig. 4. Average number of beads ingested per *Penilia* and the body length of *Penilia*.

counting the number of beads ingested is again ± 1. When the average number of beads ingested per animal is plotted against the body length (Fig. 4), it can be seen that as size increases the average number of beads ingested also increases (Table I). A least-squares line has been fitted to the data, with a P value of 0.001; the uncertainty in bead counting is ± 1, while the uncertainty in the body length measurement is estimated to be ± 50 μm.

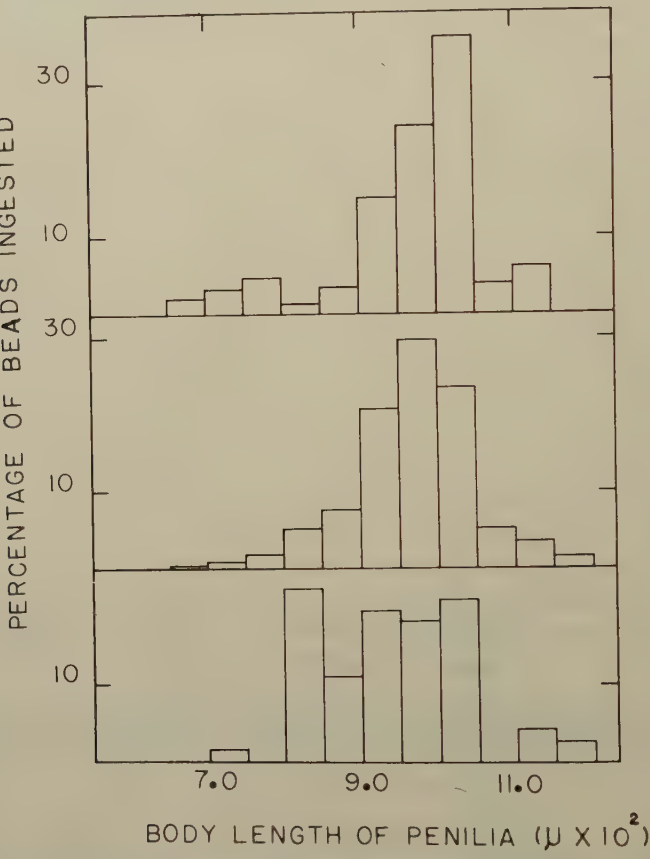

Fig. 5. Percentage of beads ingested and body length of *Penilia*: the lower histogram represents a bead size range of <1 to 20 μm, the middle one a range of 20 to 30 μm, and the upper one a range of 30 to 50 μm.

Fig. 5 shows the percentage of each bead size ingested by different sized *P. avirostris*. Both large and small animals ingest both large and small beads. It does appear from the histograms that the 800 to 1100 μm sized animals ingest more beads than larger or smaller animals. Therefore, the ingestion of different sizes of beads does not appear to be related to the size of *P. avirostris*. The statistical significance of Fig. 5 was assessed by a median test, and the results of this experiment are

also summarized in Table I. Using a two-tailed test, there was no significant difference between the size of animal and the percentage of beads ingested for the three bead size ranges shown. Throughout the experiments, no visible indication of faeces was observed.

Discussion

Penilia avirostris appears to prefer ingesting very small-sized particles (<1 to 20 μm), averaging 1.8% of the smallest size used, whereas *Acartia tonsa* (also found in Kingston Harbour), appeared to ingest plastic beads averaging 2.7% of a similar size in body (Wilson, 1973). *P. avirostris* may be competing for food by filtering smaller particles than zooplankton of comparable size. Also, by virtue of its size, greater filtering ability, and greater abundance (Gore, 1975), it may be at an advantage over smaller zooplankton competing for the smaller particles. Frequently, *P. avirostris* was the most abundant zooplankton species in Kingston Harbour, (Gore, 1975), and this may be an explanation for its success. Plastic beads are inferior to algae as a particle source as *P. avirostris* cannot break down the bead before or at the mouth. The cladoceran may reject particles of a size it could deal with in nature. However, there are many advantages in using beads, one being the ability to count accurately the particles ingested (Burns, 1968; Wilson, 1973).

Larger *P. avirostris* do not necessarily ingest only larger particles and it seems to prefer a small-sized particle whether of larger of smaller body size. These results differ from those of Burns (1968) for *Bosmina longirostris* and six species of *Daphnia*. She found that the maximum size of bead ingested continues to increase with body size. Coming from the laboratory rather than the field, these freshwater cultured cladocerans may filter and compete for food in a manner very different to that of *P. avirostris*. The larger *P. avirostris*, through virtue of their size, had a wider range of particles available to them than did the smaller animals. This should give them a "competitive advantage" (Wilson, 1973), which is apparent as more beads are ingested as the body size of the animals increases. Burns & Rigler (1967) found that the filtering rate in *Daphnia rosea* increased with body length, and Schindler (1968) noted increased ingestion in *D. magna* with age. One might expect large size to be an advantage in terms of competition for food, filtering ability, and gut capacity, particularly as all sizes were competing for the same size range of particles. In terms of animal size, there appears at first to be a rapid increase in percentage of beads ingested of the most preferred range (<1 to 20 μm). As predicted by Wilson (1975), this is followed by a broad plateau and then a decline as the body length increases, rather than each *P. avirostris* size class being of peak efficiency in a particular bead size range.

P. avirostris appeared to increase its ingestion of particles when more particles were available. This is similar to the phenomenon of superfluous feeding (Bekle-

mishev, 1961), that is, when there is an abundance of food particles, marine herbivorous zooplankton tend to ingest proportionally more particles. They may achieve this efficiency in ingestion to exploit phytoplankton blooms when available. Schindler (1968), using *Daphnia magna*, also found increased ingestion with a rise in the concentration of food. In *Penilia avirostris*, more beads were also ingested when the number of animals was increased. It is unlikely that water movement created by the activity of increased numbers of animals would make the beads more available. The proportion of beads to animals is decreased at the same time. It is more likely that stimulation of the feeding mechanism, as a result of the close proximity of large numbers of feeding animals, would cause increased intake. Because *P. avirostris* are not "pursuers" but filter particles, they do not actively select particles before they reach their appendages and mouth. In terms of Schoener's (1971) three hypotheses of optimal feeding period, it would appear that the large numbers of these animals give rise to more efficient feeding, rather than the group being of neutral value or a hindrance to feeding.

Acknowledgements

I would like to thank Professor J. Allen, Professor I. Goodbody, Dr. C. H. Barrow, and Dr. M. Itzkowitz for their valuable criticism of the manuscript.

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J. exp. mar. Biol. Ecol., 1980, Vol. 44, pp. 261–267
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NATURAL CHELATORS IN SEA WATER: DETOXIFICATION OF Zn^{2+} BY BROWN ALGAL POLYPHENOLS[1]

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Abstract: We have examined growth responses of several species of marine phytoplankton, cultured with and without heavy metal stress, to supplements of polymeric polyphenols from the brown algae *Ascophyllum nodosum* (L.) Le Jol. and *Fucus vesiculosus* L. In the absence of additional heavy metals, supplements of up to 4000 $\mu g \cdot l^{-1}$ of polyphenols had a small effect on initial growth rates for three of these microalgae and had no effect on maximum cell densities for four species. One very common, heavy metal-sensitive diatom, *Skeletonema costatum* (Grev.) Cl., showed significantly increasing maximum cell density in the cultures, with increasing addition of polyphenols to the medium. The toxicity of Zn^{2+} (0.5–2.0 $mg \cdot l^{-1}$) to cultures of the diatom *Phaeodactylum tricornutum* Bohlin was relieved by supplements (100–2000 $\mu g \cdot l^{-1}$) of the brown algal polyphenols. Exudation of these polyphenols from brown seaweeds may contribute to the natural chelating capacity of inshore sea water.

INTRODUCTION

Lucas's "ectocrine" theory of non-predatory relationships in marine ecosystems (Lucas, 1961) postulates that extracellular metabolites produced by marine organisms can influence the growth rate (and thereby the productivity, species composition, and species succession) of phytoplankton. Vitamins, toxins, and antibiotics released by certain marine organisms have been shown to exhibit direct ectocrine activity (Lefèvre, 1964; Hellebust, 1974); equally significant, however, may be "indirect ectocrine" relationships, e.g. where external metabolites affect the metal ion–chelator balance in sea water (Barber *et al.*, 1971). Because the growth of some phytoplankton may be limited by insufficiency (Anderson *et al.*, 1978) or toxicity (Sunda & Guillard, 1976; Anderson & Morel, 1978) of certain trace metal ions at ion activities occurring naturally in sea water, changes in the ion–chelator balance could be of immediate ecological significance.

[1] Issued as NRCC No. 17763.

Unidentified soluble organic compounds released by certain phytoplankton can complex (and thus detoxify) heavy metal ions (Steemann Nielsen & Wium-Anderson, 1971; Gnassia-Barelli *et al.*, 1978; Van den Berg *et al.*, 1979). Many species of phytoplankton apparently do not release such compounds (Sharp, 1977; Swallow *et al.*, 1978). Tannin-like polyphenols released by marine brown algae, Phaeophyceae (Ragan & Jensen, 1979, q.v. for further references) are potentially more important sequestering agents in many inshore waters; rates of release may exceed 1 $mg \cdot kg^{-1}$ fresh alga $\cdot day^{-1}$ (Sieburth, 1969), and polyphenol concentrations in nearshore sea water may reach 2.5 $mg \cdot l^{-1}$ (Sieburth & Jensen, 1968). These algal polyphenols chelate ions of heavy metals in vivo in specialized vacuoles called physodes (Skipnes *et al.*, 1975) and in weakly acidic aqueous solution (Ragan *al.*, 1979). We have now examined the growth responses of several species of marine phytoplankton, both with and without heavy metal stress, to supplements of polymeric polyphenols extracted from the common brown seaweeds *Ascophyllum nodosum* (L.) Le Jol and *Fucus vesiculosus* L.

Methods and Materials

Unialgal, axenic cultures of the diatoms *Chaetoceros* sp. (cf. *ceratosporum*), *Phaeodactylum tricornutum* Bohlin, *Skeletonema costatum* (Grev.) Cl. (clone Skel-5), *Thalassiosira pseudonana* (Hasle et Heimdal), and of the dinoflagellate *Amphidinium carterae* Hulb. were grown in 100-ml batches of sea-water (modified 3/4 f/10: Skjåk Bræk *et al.*, 1976) medium, from which supplementary ethylene diamine tetraacetate (EDTA) and trace metals were omitted. Sea water was collected, filtered and aged as described by Ragan & Jensen (1979). Other experimental details have been described by Jensen *et al.* (1974) and Skjåk Bræk *et al.* (1976). The culture media were supplemented (2 to 4 h before inoculation) with sterile-filtered algal polyphenols and/or zinc chloride. Concentrations of zinc ion are reported as $mg \cdot l^{-1}$ Zn^{2+} above the control levels. The algal polyphenol fractions, consisting of relatively well-defined high molecular-weight phloroglucinol-based polymers not diffusible during dialysis, were extracted and purified from *Ascophyllum nodosum* and *Fucus vesiculosus* (Ragan & Craigie, 1976; Ragan, 1976), where they constitute $\approx$15–25% of the total extractable polyphenols. The criteria of purity for this fraction have been detailed elsewhere (Ragan *et al.*, 1979). This high molecular-weight fraction contains polyphenols very similar to those exuded into sea water by living algae (Ragan, 1976).

We have used maximum rate of cell division as one measure of growth because in these experiments it invariably occurred 2–4 days after inoculation, and hence is probably relatively unaffected by nutrient limitation, auto-detoxification, autoinhibition or problems arising from natural selection (see: Barber, 1973; Sunda & Guillard, 1976). Cell morphology was monitored at intervals by microscopy.

Results and Discussion

In the first series of experiments, we examined the effect of the brown algal polyphenols on phytoplankton grown in the absence of heavy metal stress. With *Skeletonema costatum* clone Skel-5, an alga which may be "... close to its (heavy metal ion) tolerance even in plain (coastal) sea water" (Jensen *et al.*, 1974), increasing polyphenol concentrations (25 to 4000 $\mu g \cdot l^{-1}$) caused only marginal increases in initial cell division rates (Fig. 1b); the supplements, however, prolonged the periods of rapid growth, thereby moderately increasing the maximum culture densities

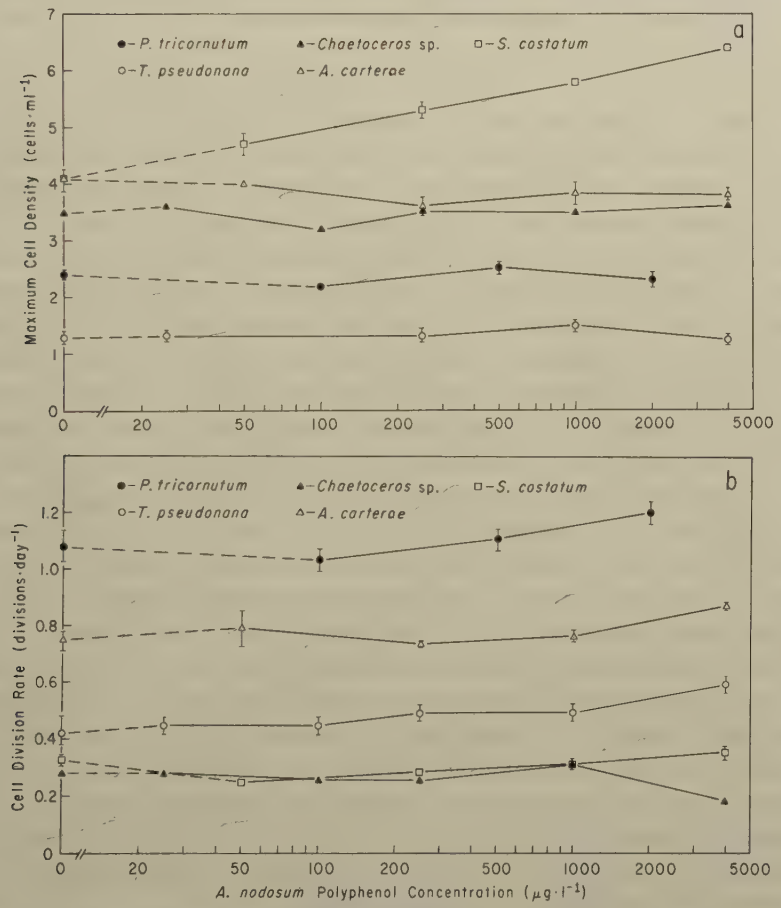

Fig. 1. Effect of *Ascophyllum nodosum* polyphenol fraction on culture density (a) and division rate (b) of five phytoplankton: cultures (from S. Myklestad) were grown at 13 °C (except *Amphidinium carterae*: 20 °C) in 250-ml silicone-coated Erlenmeyer flasks; irradiation was 55 $\mu E \cdot m^{-2} \cdot s^{-1}$ from Philips cool blue and cool white fluorescent bulbs, with a 14 : 10 h light : dark regime; cells were counted with a Celloscope model 401 (Linson, Stockholm) calibrated by haemocytometry; experimental cultures were done in duplicate, controls in triplicate; a, multiply ordinate by 10^5 (*S. Skeletonema costatum*, *Chaetoceros* sp.) or 10^6 (*Amphidinium carterae*, *Phaeodactylum tricornutum*, *Thalassiosira pseudonana*).

(cells · ml $^{-1}$) (Fig. 1a). No changes in cell morphology or size distribution were observed. *Phaeodactylum tricornutum*, which is less sensitive to Zn^{2+} and Cu^{2+} (Skjåk Bræk *et al.*, 1976), showed increased division rates with polyphenol supplements of 500 or 2000 $\mu g \cdot l^{-1}$. Polyphenol-supplemented (≥ 250 $\mu g \cdot l^{-1}$) *Thalassiosira pseudonana* reached the stationary phase in only 6 days (controls: 9–10 days). The other phytoplankton examined appeared to be relatively unaffected by polyphenol concentrations ≤ 1000 $\mu g \cdot l^{-1}$.

These results establish that the polyphenols themselves are not directly toxic to these phytoplankton under the conditions used in this study, but do not provide strong evidence either for or against the chelation hypothesis because it is possible that the heavy metals in this aged sea water were already chelated or otherwise inactivated.

To examine the chelation–detoxification hypothesis more directly, we supplemented cultures of *Phaeodactylum tricornutum* with both Zn^{2+} and the algal polyphenols. Use of the relatively insensitive *P. tricornutum* – Zn^{2+} model system (Jensen *et al.*, 1974) helped to minimize problems of residual metal ion contamination and of viability of metal-supplemented control cultures, but the results may thus tend to give a rather conservative picture of toxicity and detoxification in coastal ecosystems. The results with the *Ascophyllum nodosum* polyphenols were particularly clear (Fig. 2a); with 0.5 mg of added $Zn^{2+} \cdot l^{-1}$, all investigated polyphenol concentrations (100–2000 $\mu g \cdot l^{-1}$) significantly increased the rate of cell division. With 2.0 mg $Zn^{2+} \cdot l^{-1}$, 2000 $\mu g \cdot l^{-1}$ polyphenol were required for significant detoxification, and the toxicity of 5.0 mg $Zn^{2+} \cdot l^{-1}$ could not be relieved by any of these polyphenol supplements. Maximum culture densities were relatively unaffected except at 5.0 mg $Zn^{2+} \cdot l^{-1}$, where 10% and 25% reductions in cells · ml $^{-1}$ were observed with 500 and 2000 μg polyphenols l^{-1}, respectively. A somewhat similar, although less clear, pattern was observed with the *Fucus vesiculosus* polyphenols (Fig. 2b), except that the 2000 $\mu g \cdot l^{-1}$ supplement yielded lower division rates than did 500 $\mu g \cdot l^{-1}$.

Both the latter observation, and the unexpectedly low division rates (Fig. 2) and culture densities in the cultures treated with Zn^{2+} (5.0 mg $\cdot l^{-1}$) plus polyphenols, suggest that the polyphenols themselves (particularly those from *F. vesiculosus*) may become directly toxic to *Phaeodactylum tricornutum* at these higher metal ion activities. Heavy metal ions catalyse the oxidation of polyphenols, and phenol oxidation products are considerably more toxic to algae and higher plants than are the corresponding phenols (Stom *et al.*, 1972; Stom & Kozhova, 1976). Much higher concentrations of polyphenol-containing exudate from *Fucus vesiculosus* are toxic to phytoplankton (McLachlan & Craigie, 1964).

Other, less well characterized high molecular-weight organic fractions isolated from soils, sediments, lakes, rivers, and decaying seaweeds (Milanovich *et al.*, 1975; Prakash *et al.*, 1975; Giesy, 1976) may produce similar stimulatory effects which are often attributed to demonstrated or hypothetical metal-chelating properties. The present results suggest that the stimulatory effects of low concentrations of the

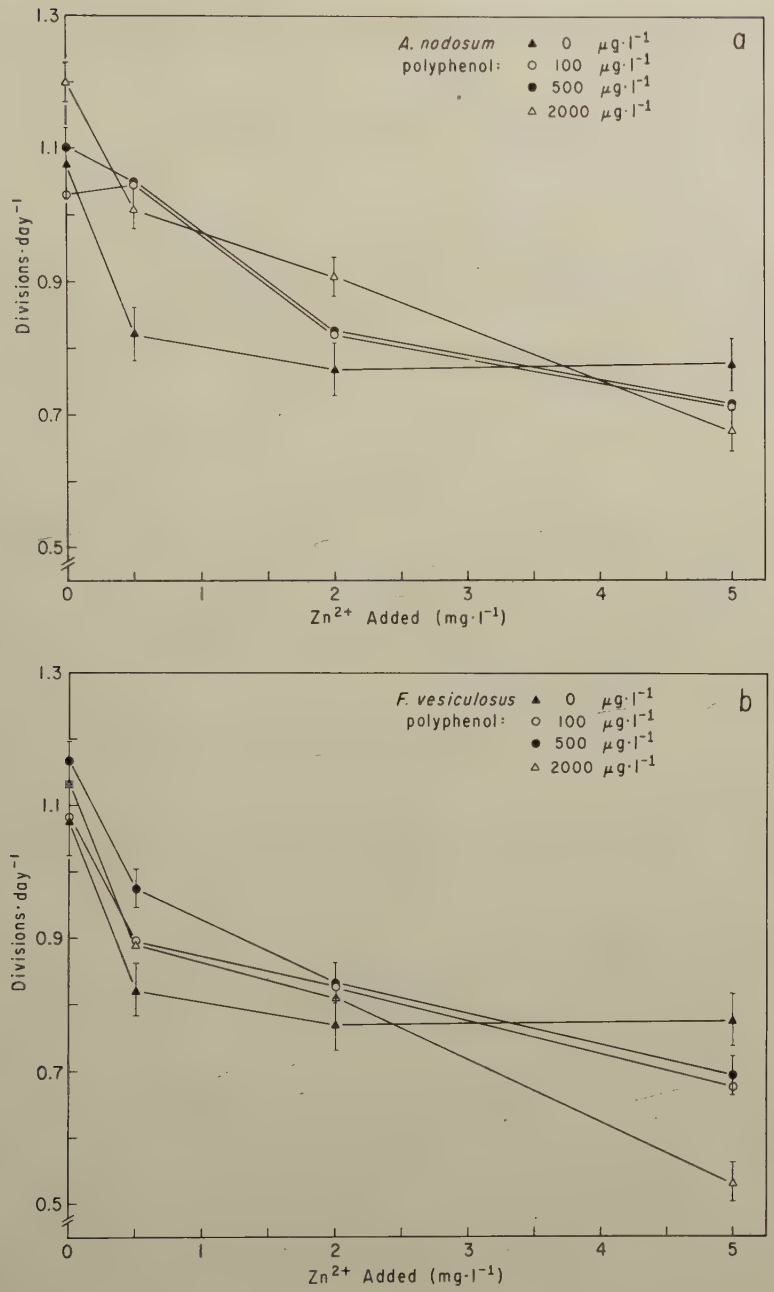

Fig. 2. Effect of Zn^{2+} plus *Ascophyllum nodosum* (a) or *Fucus vesiculosus* (b) polyphenols on division rate of *Phaeodactylum tricornutum*: error (not shown, for clarity, in some experimental points) ≈0.04 div · day $^{-1}$.

brown algal polyphenols are directly related to their ability to detoxify heavy metal ions, and lend support to earlier suggestions (McLachlan & Craigie, 1964, q.v. for further references) that these extracellular metabolites from brown seaweeds may contribute to the chelating capacity of many inshore marine waters.

Acknowledgements

We thank J. S. Craigie for critically reviewing the manuscript. Most of the experiments reported herein were conducted while M.A.R. held a National Research Council of Canada postdoctoral fellowship at the Institute for Marine Biochemistry, Trondheim.

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WATER QUALITY REQUIREMENTS FOR FIRST-FEEDING IN MARINE FISH LARVAE. I. AMMONIA, NITRITE, AND NITRATE

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Abstract: The tolerance of marine fish larvae to ammonia, nitrite, and nitrate was investigated using the decrease in first-feeding incidence following a 24-h exposure as the criterion of response. Seven species, all hatched from pelagic eggs collected at sea, were used in these experiments: two soleids (*Heteromycteris capensis* Kaup, *Synaptura kleini* (Bonaparte)), a gadid (*Gaidropsarus capensis* (Kaup)), and four sparids (*Diplodus sargus* (L.), *Lithognathus mormyrus* (L.), *Pachymetopon blochi* (Val.), and an unidentified species). Concentrations that inhibited first-feeding are compared to 24-h LC_{50}'s for the same species, and to concentrations that are known to induce lethal and sublethal responses in other teleost species. Judging from its effect on first-feeding, un-ionized ammonia is considered to be a potential hazard in the rearing tank; nitrite and nitrate are non-toxic at levels likely to be encountered in practical marine fish culture. Data are presented on the age at first-feeding and point of no return for 10 species.

INTRODUCTION

The establishment of tolerance limits of fish to pollutants (or to sub-optimal conditions) is most often experimentally achieved by relating the concentration of pollutant (or "magnitude" of sub-optimal conditions) to some measurable, presumably deleterious, response. Primarily for reasons of simplicity, the response of choice has traditionally been death, within a stated exposure period. When one is concerned with the growth rate of fish in a tank, or the long-term health of a natural population, more subtle, sublethal responses are more meaningful. A considerable number of useful sublethal responses have been suggested, and many of these have been exploited, for use in toxicity studies (Waldichuk, 1973; Rosenthal & Alderdice, 1976).

In the present study, the inhibition of first-feeding was chosen as the response, ammonia, nitrite, and nitrate were tested as potential inhibiting factors. Low and high pH, dissolved oxygen, and carbon dioxide have been tested in a similar manner (Brownell, 1980). That the first-feeding stage is among the more sensitive to sub-optimal conditions is suggested by even the large number of published failures of investigators to rear marine fish larvae beyond that stage in the laboratory. Of course, failure in many of these cases can as easily be attributed to the unavailability of a satisfactory food. Nevertheless, in their review of sublethal effects of environ-

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mental stressors on marine fish eggs and larvae, Rosenthal & Alderdice (1976) concluded: "Available data suggest that several stages in the life cycle of marine fishes are more susceptible to environmental and pollutional stress. These are a) gonadal tissue, b) the highly plastic early embryo, and c) the stage of larval transition between reliance on endogenous and exogenous sources of food."

A decline in food consumption or "loss of appetite", among fish during periods of stress has been recorded by many authors. Examples of feeding inhibition in several species of marine fish larvae may be found in the literature (Wilson, 1972; Alderson, 1972; Struhsaker *et al.*, 1974; Blaxter, 1977). Eldridge *et al.* (1977) reported increased food consumption and growth among Pacific herring larvae exposed to low concentrations of benzene. The use of the first-feeding response in evaluating the potential of a parcel of water to support survival of marine fish larvae was pioneered by Lasker (1975).

Ammonia can be expected to occur wherever fish are reared. Although significant amounts of other protein catabolites may also be released, ammonia is the major form of excreted nitrogen in teleost fish, in the invertebrates that are commonly maintained in rearing tanks as food, and in the bacteria living heterotrophically on nitrogenous substrates. The literature on the toxicity of ammonia to fish has been reviewed several times (e.g., Doudoroff & Katz, 1950; EIFAC, 1970), but information on marine species is scanty. Some data on the tolerance of two marine pleuronectids (presumably juveniles or adults) to un-ionized ammonia have been published (Hampson, 1976), and three euryhaline species have been tested in sea water (Herbert & Shurben, 1965; Hazel *et al.*, 1971). Although limited information is available on the effect of ammonia on the eggs and larvae of a few freshwater fish species (particularly salmonids), none was found on the tolerance of the eggs and larvae of marine fish.

Nitrite is of interest to biologists involved with recirculating fish-culture systems because it is an intermediate in the bacterial nitrification of ammonia. The most recent review on the effects of nitrite on fish (Russo & Thurston, 1977) reveals a surprising variability in tolerance, from species to species and from publication to publication. Much of this variability can be explained by differences in the ionic constitution of the dilution waters used in tolerance tests. Weber (1966) noted a decrease in nitrite toxicity when Ca^{2+} was added to the dilution water; Russo & Thurston (1977) and Perrone & Meade (1977) found a similar decrease when Cl^- was present. Crawford & Allen (1977) reported a dramatic increase in the tolerance of chinook salmon (*Onchorhynchus tshawytscha*) to nitrite in sea water, as opposed to fresh water.

Aside from the paper by Crawford & Allen, the reference by Wickins (1976) to a personal communication from R. Alderson noting a greater resistance of turbot (*Scophthalmus maximus*) to nitrite than freshwater fish, and a few unreferenced assertions in the popular aquarist literature, no published information appears to be available on the effect of nitrite on any stage of marine fish.

The origins and consequences of nitrate in recirculating marine culture systems were treated briefly by Kinne (1976). The tolerance of juvenile and adult freshwater fish to nitrate has been studied by several authors (e.g., Trama, 1954; Westin, 1974; Colt & Tchobanoglous, 1976). The youngest fish for which data are available appear to be the 6–11 mm guppies (*Poecilia reticulata*) tested by Rubin & Elmaraghy (1977). Braun (1972, cited by Bohl, 1977) associated a loss of appetite with high nitrate concentrations. The sensitivity of early stages of marine fish to nitrate has apparently not been investigated.

Supply and Handling of Larvae for Experimental Purposes

The fish larvae used in this study came entirely from sea-spawned, pelagic eggs collected by plankton net off the Cape of Good Hope. All tows were made at the sea surface within ≈3 km from shore. Collecting gear and procedures have been described elsewhere (Brownell, 1979). On return to the laboratory, the eggs were picked out by pipette with the aid of a dissecting microscope, identified to species (when possible), and distributed among a number of incubation baskets floating in the water table of an 850-l closed-circulation system. Experimentation was conducted in the constant temperature room (15 °C) that housed the closed-circulation system.

Filtered (25 μm), natural sea water, collected from Three Anchor Bay, Cape Town, was used in the system. A summary of the analytical results obtained during two years of use is presented in Table I. Distilled water was added to compensate for evaporative loss; NaOH and $NaHCO_3$ were added to adjust pH and alkalinity, respectively.

The incubation basket (≈75 ml) is a truncated cone of nylon mesh attached to a Perspex collar surrounded by a styrofoam float ring. Eggs floating at the surface come in contact with the Perspex collar rather than the mesh, and are thereby

Table I

Some physical, chemical, and biological characteristics of sea water in the closed circulation system (dilution water): where applicable, the range of measured values is given.

Total volume	800–900 l	Total ammonia-N	15–66 $\mu g \cdot l^{-1}$
Flow rate	1.5–2.5 l · min^{-1}	Nitrite-N	1.3–2.0 $\mu g \cdot l^{-1}$
Temperature	14.8–15.2 °C	Nitrate-N	0.14–1.50 mg $\cdot l^{-1}$
Salinity	34.4–35.7‰ *S*	Reactive phosphate-P	50–130 $\mu g \cdot l^{-1}$
pH	7.79–7.85		
Total alkalinity	2.15–2.45 meq $\cdot l^{-1}$	Reactive silicate-Si	22–500 $\mu g \cdot l^{-1}$
Free CO_2-C	0.37–0.47 mg $\cdot l^{-1}$		
Dissolved O_2	7.9–8.1 mg $\cdot l^{-1}$	Illumination at water surface	300 lux
Bacteria (suspended):	plate count (ZB2216E medium): $3.4 \times 10^3 - 4.8 \times 10^5$ cells · ml^{-1} direct count (fluorescence): $6.4 \times 10^5 - 9.5 \times 10^5$ cells · ml^{-1}		

not left stranded if the basket is jarred. The mesh and Perspex are stained black, and the water table is lined with black polyethylene. When the room lights are extinguished, eggs and hatchlings are readily visible in the beam of a hand-held 6-V microscope lamp. Up to ≈100 eggs were placed in each basket, and their progress was monitored at 12-h intervals. Larvae having hatched during the previous 12 h were carefully removed by pipette and transferred to larger (1-l) baskets, also made from 200-μm nylon mesh suspended from a styrofoam float ring. The time of hatch was recorded as the midpoint of two successive checks. The bottom of the larva baskets consists of a disc of white plastic against which eyed larvae are visible.

Experimental Feeding Containers

Tolerance testing was conducted in 350-ml, transparent containers (Fig. 1a). The cylindrical portions are clear Perspex, the front and back walls are glass. The bung (Fig. 1b) is made from a 3-cm section of 2.5-cm o.d. Perspex tubing; one end is slightly flared and covered by nylon screen of 200 μm pore size. When the bung is pressed just far enough into the neck of the container to make contact between

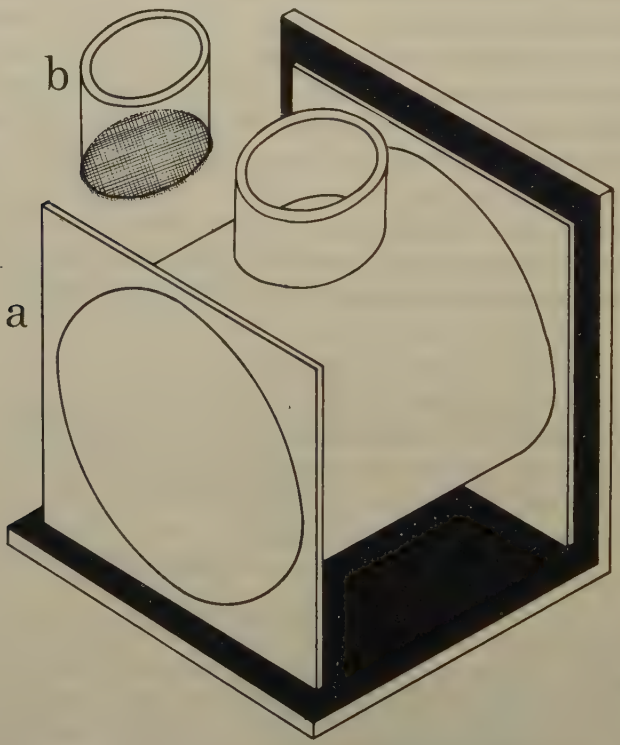

Fig. 1. Diagram of experimental feeding containers: a, 350-ml feeding container on black stand; b, screened bung.

the mesh and the water surface, the container can be turned in any direction without leaking. During tests, they were always turned so that the glass faces were in a horizontal position. This eliminated the likelihood of larvae concentrating in the neck of the container (which tended to occur in an upright position), and it seemed to improve feeding, perhaps by reducing glare or irregular scattering of light within the container.

Larvae could be examined undisturbed with a horizontally positioned binocular dissecting microscope through the flat glass wall. To simplify manoeuvering the microscope, a system employing an overhead beam and counter-weights was devised.

Age at First-feeding Curves

To study the effects of various environmental factors on first-feeding success, it was first necessary to determine, with reasonable accuracy, when first-feeding could be expected to occur. This involved constructing a curve for each species, relating the percent of larvae feeding to the age of the larvae tested. Previously unfed larvae of known (within 6 h) age were pipetted from larva baskets into a feeding container holding $\approx$300 ml of system water. A concentrated suspension of cultured prey organisms (rotifers *Brachionus plicatilis* or *Proales* cf. *similis*) in system water was added to give a final density of $\approx$15 (10–20) particles/ml. The container was then gently topped up with system water, the screened bung fitted, and the container laid face-down on a black feeding stand under 3000 lux fluorescent lighting. The larvae were exposed to food for 4 h and then examined with the suspended microscope. One by one, they were rated "fed" or "unfed" and removed from the container by pipette. Larvae that had only 1–2 *Brachionus* or 1–4 *Proales* in the gut at the end of 4 h were not considered as having fed adequately and were included in the "unfed" category. For analysis, test ages were grouped among a number of age classes of 8 h duration, and the percent of larvae in each group rated "fed" was plotted against the midpoint of each age-class on probability-linear graph paper. Three straight lines were first fitted by eye to the resulting distribution of points: an ascending line, corresponding to an initial increase in first-feeding success with age; a horizontal line, corresponding to the phase of optimal first-feeding; and a descending line, corresponding to the decrease in first-feeding success associated with the point of no return (PNR) phenomenon. The data contributing to the ascending and descending lines were analysed by a probit technique (Finney, 1971); the horizontal line was fixed by dividing the number of feeding larvae in the groups that contributed to that line by the total number of larvae tested in the same groups.

Three values were extracted from these curves: (1) the age at onset of first-feeding, (2) the age at optimal first-feeding, and (3) the age at PNR. The age at onset of first-feeding is defined here as the time interval between hatching and the point when 50%

of those larvae that would be expected to feed during the phase of optimal first-feeding (under stated conditions) actually feed. The age at PNR is the time interval between hatching and the point when 50% of those larvae that would have been expected to feed during the phase of optimal first-feeding are no longer capable of first-feeding. The age at optimal first-feeding is defined as the arithmetic mean of the age at onset of first-feeding and the age at PNR. The application of this terminology to first-feeding Cape rockling is depicted in Fig. 2. Information on feeding ages of 10 species is presented in Table II.

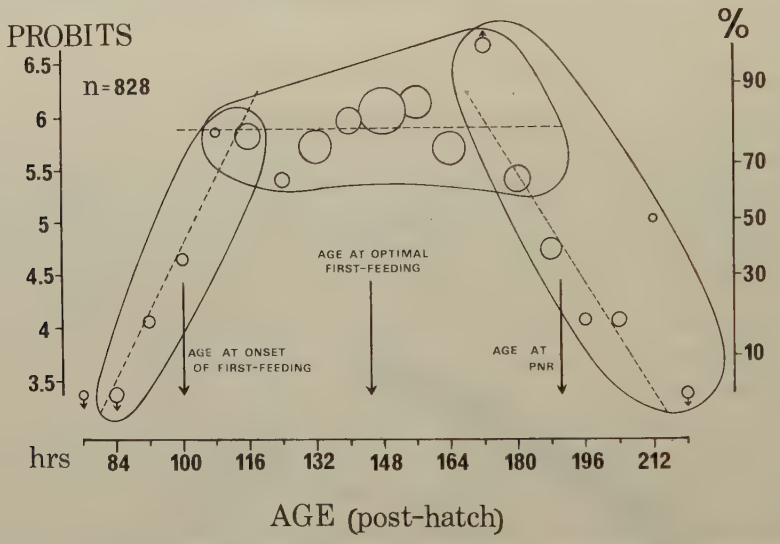

Fig. 2. Age at first-feeding curve for *Gaidropsarus capensis* feeding on *Brachionus plicatilis*: circles represent raw data, their areas are proportional to the number of larvae tested in the respective age class; solid lines surround those circles that were considered to contribute to the corresponding dashed lines.

Tolerance Studies

General Methods

Larvae to be used in tolerance tests were pipetted from their larva baskets approximately 26 h prior to the calculated age at optimal first-feeding for that species (Table II). A kind of randomness in apportioning available larvae to control and treatment test containers was achieved by very gently stirring the water in the floating basket, then drawing out a few larvae at a time, filling all the containers more or less simultaneously. The containers were fitted with screened bungs, turned face-down, and left undisturbed for 24 h. A count was then made of mortalities (with death defined as a whitening of the tissue) with the aid of the suspended microscope. A concentrated suspension of rotifers was distributed about equally

TABLE II

Age at first-feeding data and other information relevant to the first-feeding tolerance tests: ages in parentheses are estimates; insufficient data were collected to warrant the fitting of curves; PNR, point of no return.

Species	Age at onset of first-feeding	Age at PNR	Age at optimal first-feeding	Minimum and maximum age at beginning of 24-h exposure to test water	Minimum and maximum age at beginning of 4-h exposure to food	Experimental food
Congiopodus spinifer (Smith)	(36)	(>170)	(100)	62–86	86-110	*Brachionus*
Diplodus sargus (L.)	136	210	173	135–159	159–183	*Proales*
Gaidropsarus capensis (Kaup)	100	190	145	107–131	131–155	*Brachionus*
Heteromycteris capensis Kaup	134	212	173	135–159	159–183	*Brachionus*
Lithognathus mormyrus (L.)	140	204	172	134–158	158–182	*Proales*
Pachymetopon blochi (Val.)	130	204	167	129–153	153–177	*Brachionus*
Pterosmaris axillaris (Boulenger)	145	(>240)	(190)	152–176	176–200	*Brachionus*
Synaptura kleini (Bonaparte)	118	189	154	116-140	140-164	*Brachionus*
Trulla capensis Kaup	(140)	(190)	(165)	127–151	151–175	*Proales*
Species 5 (unidentified)	127	216	172	134–158	158–182	*Proales*

among the containers, without removing the screened bung, to yield a final concentration of 15 (10–20) rotifers/ml. By withdrawing the bung just far enough to trap the additional fluid, the containers could once again be turned on their sides without leaking. They were then placed on a black stand for a period of 4 h under fluorescent lighting providing 3000 lux at the level of the containers. Finally, the containers were righted, the bung removed, and the larvae were examined with the suspended microscope, evaluated according to the gut-fullness rating system described above, and removed one at a time by pipette. For various reasons, the methods used in certain tolerance tests were more complex than those just described. Additional information is provided below.

When large hauls of eggs were taken in the plankton, there were sometimes sufficient numbers of larvae hatching during a single 12-h interval to make up an entire treatment series and control. When material was less abundant, one or more of the planned treatment tests was dropped, and those tests were completed with larvae from another 12-h interval, or even from another collection of eggs. No tolerance tests were conducted, however, without simultaneous controls, consisting of larvae taken in the same collection and hatched during the same 12-h interval as the treatment larvae.

Feeding incidence in control groups usually varied, sometimes quite noticeably, from one batch to another. A series was rejected whenever control feeding incidence fell below an arbitrary 50%. Batches with different control feeding incidences were rendered comparable by making the assumption that the percent decrease in feeding incidence in treatment groups (relative to the control group) is strictly a function of the concentration of inhibiting substance, and is not related to the incidence of feeding in the control group. In fact, based on correlation analyses of cases where the same concentration of inhibitor was tested on more than one batch of the same species, the assumption may be justified: there was no statistical evidence that batches in which first-feeding incidence was high in the control group fed disproportionately better under sub-optimal conditions in treatment groups.

Response curves were fitted by probit analysis (Finney, 1971). The estimate of the natural response rate was based entirely on control feeding incidence. When data from more than one batch were combined, the estimate of the natural response rate was based on the weighted, mean feeding incidence of all control groups involved. At any treatment concentration where data from more than one batch were combined, each batch was corrected independently for natural responsiveness (using the control feeding incidence of that batch) before a weighted, mean feeding incidence for the treatment concentration was calculated.

For each combination of fish species and variable tested, four values, with their respective 95% confidence limits, were extracted from the calculated response curves: (1) 24-h LC_{50} (concentration of the variable that kills 50% of the larvae during a 24-h exposure), (2) 24-h LC_{10} (concentration that kills 10%), (3) 24-h first-feeding EC_{50} (concentration that reduces first-feeding incidence by 50% after a 24-h exposure),

(4) 24-h first-feeding EC_{10} (concentration that reduces first-feeding incidence by 10%). Note that exposure to sub-optimal conditions continued during the 4-h feeding test.

AMMONIA

Specific methods

Known volumes of a concentrated (4.19 M) NH_4Cl solution, measured by micropipette, were mixed with freshly-drawn system water to yield a graded series of test solutions. The proportion of ammonia in the un-ionized form was calculated independently (Whitfield, 1974) for each treatment, based on the pH (NBS) measured after larvae were removed from test containers. The 95% confidence limits of the response curves were expanded by a value of 8% of the predicted mean effective concentration at any response percentile to account (in an approimate way) for uncertainty in the true concentration of un-ionized ammonia to which larvae were exposed. About 70% of the uncertainty arose from pH instrumentation error and error in the ionization constant of ammonium. Response curve calculations were based on a log normal model of tolerance distribution.

Results and discussion

The results of the ammonia experiments are summarized in Table III. Five species of first-feeding larvae (one gadid and four sparids) were tested; only the response curve for the gadid is presented in graphical form (Fig. 3). Based on inspection of the five response curves, the author would predict the maximum concentration of un-ionized ammonia that negligibly affects first-feeding following a 24-h

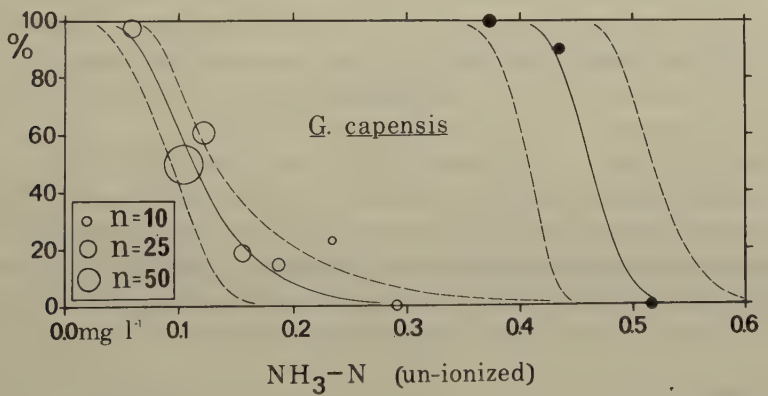

Fig. 3. Response of first-feeding *Gaidropsarus capensis* to un-ionized ammonia: open circles represent raw data (adjusted for natural responsiveness) on first-feeding incidence following 24-h exposure to various ammonia concentrations; solid circles represent data on percent survival during 24-h exposure; the areas of the circles are proportional to the number of larvae tested at corresponding ammonia concentrations; the 95% confidence limits are represented by dashed lines.

TABLE III

Summary of tolerance limits: ammonia is expressed in mg · l $^{-1}$ NH_3-N (un-ionized), nitrite in mg · l^{-1} NO_2-N, nitrate i mg · l^{-1} NO_3-N; 95% confidence limits are in parentheses.

Variable	Species	24-h first-feeding EC_{50}	24-h first-feeding EC_{10}	24-h LC_{50}	24-h LC_{10}	LC_{50}/EC_5
NH_3	*Gaidropsarus capensis*	0.11 (0.09–0.13)	0.07 (0.05–0.09)	0.46 (0.41–0.52)	0.43 (0.38–0.48)	4.1
	Diplodus sargus	0.10 (0.06–0.15)	0.03 (0.01–0.08)	0.36 (0.31–0.42)	0.29 (0.24–0.34)	3.8
	Lithognathus mormyrus	0.16 (0.11–0.22)	0.07 (0.04–0.10)	0.38 (0.33–0.42)	0.34 (0.29–0.38)	2.4
	Pachymetopon blochi	0.22 (0.17–0.28)	0.13 (0.10–0.16)	0.42 (0.36–0.48)	0.38 (0.31–0.46)	1.9
	Species 5 (Sparidae)	0.16 (0.11–0.23)	0.10 (0.07–0.15)	0.40 (0.34–0.47)	0.35 (0.28–0.42)	2.5
NO_2^-	*Gaidropsarus capensis*	450 (380–530)	280 (220–350)	2210 (1900–2560)	1500 (1210–1870)	4.9
	Synaptura kleini	350 (250–500)	180 (100–350)	2110 (1670–2670)	1210 (870–1690)	6.0
	Heteromycteris capensis	340 (270–440)	190 (120–280)	2440 (2200–2690)	2170 (1900–2480)	7.1
	Lithognathus mormyrus	360 (260–480)	60 (20–190)	1230 (1020–1470)	670 (570–790)	3.5
	Diplodus sargus	330 (270–410)	150 (90–240)	1360 (1170–1590)	870 (770–990)	4.1
NO_3^-	*Gaidropsarus capensis*	1020 (770–1520)	360 (170–510)	>4000		4^+
	Heteromycteris capensis	710 (590–870)	420 (330–540)	5050 (3730–6850)	3510 (2820–4380)	7.1
	Diplodus sargus	780 (510–1200)	270 (150–480)	3560 (2920–4350)	3100 (2510–3820)	4.6
	Lithognathus mormyrus	600 (470–760)	270 (210–360)	3450 (3260–3660)	3020 (2800–3250)	5.8

exposure to lie between 0.02 and 0.05 mg · l $^{-1}$ NH_3-N (un-ionized). At 15 °C, 35‰ *S*, and pH 7.85, this would correspond to a total ammonia concentration of 1.4 to 3.4 mg · l^{-1} N. Ammonia levels of this magnitude are rapidly attained in an overloaded culture system.

The 24-h LC_{50}'s for the five species ranged from 0.36 to 0.46 mg · l^{-1} NH_3-N, which compares with 24-h LC_{50}'s published for the more sensitive freshwater juvenile and adult fish (e.g., salmonids). Based on LC_{50}'s (Rubin & Elmaraghy, 1977), guppy fry appear to be considerably more tolerant of un-ionized ammonia than these first-feeding marine larvae.

NITRITE

Specific methods

Treatment solutions were prepared by mixing quantities of a concentrated stock solution of $NaNO_2$ (4.70 M), measured by micropipette, with system water. No dose-

uncertainty adjustments were made to confidence limits of the curves. A log normal distribution of tolerance was assumed.

Results and discussion

Five species were tested for nitrite tolerance: a gadid, two soleids, and two sparids (Table III). The 24-h first-feeding EC_{50}'s ranged from 330 to 450 mg·l^{-1} NO_2-N, with 95% confidence limits ranging from 240 to 530 mg·l^{-1}. 24-h LC_{50}'s for all five species were between 1230 and 2440 mg·l^{-1}, with the gadid and soleids, as usual, yielding a higher value for acute lethal toxicity than the sparids.

The contrast between these figures and those of salmonids tested in fresh water of low dissolved solids (e.g., a 96-h LC_{50} of 0.23 mg·l^{-1} NO_2-N reported by Brown & McLeay, 1975) is astounding. Even the salmon tested by Crawford & Allen (1977) in sea water exhibited less tolerance than the above larvae: those authors reported a 10% mortality after a 48-h exposure to 326 mg·l^{-1} NO_2-N.

A few papers have reported nitrite concentrations in tanks where marine fish were being reared. Riley & Thacker (1963, Fig. 5) showed nitrite concentration peaking at about 0.05 mg·l^{-1} (= 3.7 μg-at.·l^{-1}) NO_2-N towards the end of a plaice-rearing experiment. This value falls just within the range (0.01-4 μg-at.·l^{-1}) found in oceanic surface waters (Kinne, 1976). Barnabé (1976, table II) measured nitrite concentrations of only 0.005–0.023 mg·l^{-1} N in a tank where larval seabass were being reared. Even when 5 g of mussel flesh was allowed to decompose in an 8-l tank of static sea water, nitrite only reached 12.2 mg·l^{-1} N. In a similar tank under constant aeration, the NO_2– concentration peaked at 15.2 mg·l^{-1} (Kühl & Mann, 1956). A nitrite concentration of even 50 mg·l^{-1} N had no measureable effect on first-feeding in this study. It is highly unlikely that levels of this magnitude would ever be produced in a rearing tank if any attention, whatsoever, is paid to hygiene and water quality.

NITRATE

Specific methods

Treatment solutions were prepared by mixing quantities of a concentrated stock solution of $NaNO_3$ (4.60 M), measured by micropipette, with system water. No dose-uncertainty adjustments were made to confidence limits of the curves. A log normal distribution of tolerance was assumed.

Results and discussion

First-feeding larvae of four species were exposed to various nitrate concentrations: one gadid, one soleid, and two sparids (Table III). All four species proved to be tolerant of very high nitrate levels, the 24-h first-feeding EC_{50}'s ranging from 600 to

1020 mg $\cdot l^{-1}$ N, and 24-h LC_{50}'s from 4200 to 8700 mg $\cdot l^{-1}$. Substantial accumulations of nitrate (e.g., Oliver, 1957: 310 mg $\cdot l^{-1}$ NO_3-N) have been reported in marine aquarium systems after many years of water re-use, seemingly without deleterious effects on the inhabitants of the systems. Such concentrations are easily controlled, however, by partial water changes, and should pose no hazards to the marine fish nurseryman.

Freshwater fish have yielded 24-h and 96-h LC_{50}'s in the range 1–2 g $\cdot l^{-1}$ NO_3-N when $NaNO_3$ is the source of nitrate (e.g., Trama, 1954; Westin, 1974; Colt & Tchobanoglous, 1976). In those cases, much of the toxic effect must be attributed to the high osmolarity of the treatment solutions. Because of the high concentration of the nitrate stock solution used in the present study (4.60 M), the salinity of the test water also exceeded that of the controls. The concentration of total dissolved solids at nitrate levels that resulted in a 50% reduction in first-feeding ranged from 39 to 41‰ *S*; 24-h LC_{50} salinities ranged from 59 to 83‰. The salinity of the control water was 35‰. In a single experiment designed to compare the response of larvae to chloride-enhanced salinities equivalent to the nitrate-enhanced salinities just mentioned, the author tested first-feeding and survival in the Cape sole (*Heteromycteris capensis*) following 24-h exposure to NaCl-enriched seawater solutions of 40, 50, and 70‰ *S*, in addition to the control of 35‰ *S*. At 40‰ *S*, first-feeding incidence was 96% that of the control, suggesting negligible impairment of first-feeding at this salinity. At 50‰ *S*, feeding incidence was 59% that of the control, which was shown by a χ^2 test to be significantly ($P < 0.05$) less. These data show that, in the present study, feeding inhibition observed in nitrate solutions below a concentration of ≈ 1 g $\cdot l^{-1}$ (equivalent to a salinity of 40.5‰) cannot simply be attributed to the osmolarity of the test water. The fact that there was 15% mortality in NaCl-enriched solutions of 50‰ *S* (none in the control), and 100% ($n = 20$) at 70‰ *S*, however, implies that the *lethal* toxicity of nitrate, in the present study, can just as easily be attributed to elevated salinity.

General Discussion

Certain nitrogenous metabolites and their derivatives, particularly ammonia, nitrite, and nitrate, can fluctuate widely in recirculated water, and it is useful to know what levels of these substances are likely to cause concern in a marine fish hatchery/nursery operation. Of these three variables, only un-ionized ammonia poses a material hazard. Nitrite and nitrate affect first-feeding success only at concentrations well above those expected to occur naturally in practical marine pisciculture.

The first-feeding response can be a powerful tool in establishing criteria for survival of fish larvae. Lasker (1975) used it to assay the availability of food for larval northern anchovy (*Engraulis mordax*) at sea. The two principal advantages of using

this stage, rather than later stages, are that (1) the gut is empty at the beginning of the experiment, obviating the need for a preliminary period of starvation or labeling of food, and (2) the pre-test history of the larvae can be more confidently controlled, thus increasing the likelihood of using uniformly healthy experimental animals. The two principal disadvantages of using the first-feeding stage are (1) the extreme fragility of the larvae, and (2) the necessity of timing the feeding test between the point when the larvae are mature enough to first-feed and the point when first-feeding success begins to decline because of starvation-induced degeneration. This period is highly temperature- and species-dependent, and must, therefore, be carefully determined in advance. Such factors as the size and shape of the test container, the amount and direction of light, and the degree of contrast between the food and the background, can be as important as the food itself.

Twenty-four hours (rather than 48, 96, or even the entire interval between hatching and first-feeding) was chosen as the standard duration of exposure to test conditions in this study. The rate of development of fish eggs and larvae is very often altered, sometimes accelerated but usually retarded, under adverse conditions. Rosenthal & Alderdice (1976) review such effects in marine teleost eggs and larvae; many more examples are available in the freshwater literature. Because timing of the first-feeding test was so critical, any differential developmental acceleration or retardation between control and treatments, or even between treatments, would have greatly complicated the interpretation of results. It was assumed that a 24-h exposure would sufficiently affect first-feeding incidence to provide a useful indication of tolerance, and at the same time, cause minimal alteration of the age at optimal first-feeding. The choice of 4 h as a standard period of exposure to food was based on a series of experiments (Brownell, unpubl.) that demonstrated that over 90% of larvae that feed by the end of an 8-h exposure to food have already fed by the end of the fourth hour.

The food organisms (rotifers) used in feeding tolerance experiments underwent no acclimation, either to system water or to the presumably sub-optimal conditions prevailing in treatment containers. The assumption made here was that the availability and attractability of the rotifers as food for larvae were not significantly affected by the test solutions. In fact, no differences in the distribution of rotifers in the control and various treatment containers were detectable by eye. Apparently even the degree of phototaxis and thigmotaxis expressed by the rotifers was not noticeably affected by the test concentrations employed. The remarkable tolerance of *Brachionus* and *Proales* to short-term exposure to elevated levels of nitrogenous metabolites does not seem unique among rotifers (Buikema *et al.*, 1974).

The inhibition of first-feeding is probably not the most sensitive indicator of stress in fish larvae. No doubt much more sensitive behavioural or physiological responses will eventually be recognized. It is, nevertheless, a highly relevant response, in that death by starvation is the inevitable consequence.

Acknowledgements

I thank the people whose chemical and bacterial analyses contributed to Table I, namely, S. Mostert, J. Henry, K. Trotter, H. Mazure, and A. Linley. R. Pourriot identified the rotifer, *Proales*, and R. Griffiths supplied algal cultures. I am grateful to A. Brown, J. Field, and H. Champion for their advice and encouragement. I especially thank A. Brown for facilitating the publication of this and other papers in my absence. The generous sponsorship of this project by the Fisheries Development Corporation of South Africa is very gratefully acknowledged.

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J. exp. mar. Biol. Ecol., 1980, Vol. 44, pp. 285–298
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WATER QUALITY REQUIREMENTS FOR FIRST-FEEDING IN MARINE FISH LARVAE. II. pH, OXYGEN, AND CARBON DIOXIDE

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Abstract: Previously unfed larvae representing eight species of marine teleosts (a soleid, *Heteromycteris capensis* Kaup; a cynoglossid, *Trulla capensis* Kaup; a gadid, *Gaidropsarus capensis* (Kaup); a congiopodid, *Congiopodus spinifer* (Smith); three sparids, *Diplodus sargus* (L.), *Pachymetopon blochi* (Val.), and an unidentified species; and a centracanthid, *Pterosmaris axillaris* (Boulenger)) were exposed for 24 h to various pH's and concentrations of dissolved oxygen and carbon dioxide and then tested for their ability to first-feed. Mortalities recorded during the 24-h exposure went into the fitting of response curves and the calculation of the LC_{50} and LC_{10}. The incidence of successful first-feeding during the subsequent 4-h exposure to food yielded values for the EC_{50} and EC_{10}. The exposure to sub-optimal conditions continued during the 4-h feeding test. The sensitivity of first-feeding larvae to high pH and dissolved oxygen may pose hazards for the marine fish culturist; low pH appears to be harmful (at least in the short term) only at levels below about pH 6.0; carbon dioxide poisoning is of doubtful importance in practical fish culture. There were only minor interspecific differences in calculated 24-h first-feeding EC_{50}'s, which suggests general applicability of the results to a wide variety of first-feeding marine fish larvae.

INTRODUCTION

The kinds of environmental stressors which, at present, are of particular interest to the intensive mariculture manager or engineer are those that originate with the cultured organisms themselves, or with their food. It is these stressors that determine water re-use rates, stocking densities, and other factors relating to water quality management. Low and high pH, low dissolved oxygen, and high carbon dioxide are examined in this study with the object of identifying and quantifying those that are likely to cause concern in a marine fish hatchery/nursery operation. Ammonia, nitrite, and nitrate were examined previously (Brownell, 1980).

The decline in the pH of recirculated water is chiefly attributable to the bacterial oxidation of excretory ammonia. From the stoichiometries of the reactions involved, Wickins (1976) calculated that the oxidation of 1 mg of nitrogen as NH_4^+ to nitrogen as NO_3^- requires 4.27 mg O_2 and 0.09 mg inorganic C, and produces 0.14 mg H^+. The decrease in pH is compounded by a simultaneous loss of carbonate alkalinity and consequent decline in the buffering capacity of the recirculated water.

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The sensitivity of freshwater fish to low pH has been extensively studied (Doudoroff & Katz, 1950; EIFAC, 1968). Requirements for survival through egg and larval stages were still poorly known at the time of the EIFAC review. This gap has since largely been filled for freshwater fish.

The pH of oceanic surface waters in equilibrium with atmospheric carbon dioxide rarely falls below 8.1; the extreme of pH 7.5 is generally restricted to oxygen minimum zones, usually at depth (Sverdrup *et al.*, 1942). Without evidence to the contrary, one could easily accept the notion (Jones, 1964, p. 107) that marine fish are markedly less tolerant of low pH than freshwater fish. Although the response of certain marine fish (including early stages) to low pH has been studied (e.g., Bishai, 1960) it is not possible, from the published reports, to establish whether the observed effects were due to hydrogen ion concentration or to free carbon dioxide produced by the acidification of sea water.

Several investigators have published support for the increasingly widespread practice of rearing the early stages of marine fish in the presence of one or more species of planktonic algae (e.g., Alderson & Howell, 1973). The observed enhancement of survival and growth of the larvae has been attributed to various mechanisms (Struhsaker *et al.*, 1973), among them that phytoplankton provides food for the herbivorous zooplankters on which the fish are fed; that it extracts nitrogenous metabolites, e.g., ammonia, that could otherwise reach harmful levels; that it releases anti-bacterial, or even growth-enhancing substances into the rearing water. The effect of phytoplankton growth of interest here is the increase in pH that is brought about indirectly by the extraction of free carbon dioxide from the water.

Publications on the tolerance of freshwater fish to high pH have been reviewed by Doudoroff & Katz (1950), Jones (1964), and EIFAC (1968), among others. The literature includes several reports on the tolerance of eggs and larvae of both freshwater and marine species (e.g., Schach, 1939; Kelley, 1946; Bishai, 1960).

Reviews of the literature on the dissolved oxygen (DO) requirements of fish have been compiled by Doudoroff & Shumway (1970) and Davis (1975), among others. Marine fish have received only a fraction of the attention devoted to freshwater species. Available data on the response of marine fish larvae to low DO come almost entirely from Bishai (1959), Deubler & Posner (1963), Saksena & Joseph (1972), De Silva & Tytler (1973), and Sylvester *et al.* (1975). None of these studies was concerned with the effect of reduced DO on food intake.

From the literature on the DO requirements of various stages in the life cycles of teleost fish, it can be concluded (though not entirely without reservation) that the period beginning just prior to hatching and ending with the development of branchial respiration is the most sensitive to low DO. Such a period is present in most marine and freshwater teleosts with small eggs. There are several indirect reasons to suspect that marine fish larvae relying on cutaneous respiration would be particularly sensitive to low DO, and that this sensitivity would be aggravated in culture. (1) It is during the early feeding stages that maximal density of food is

required, which contributes to the biological oxygen demand of the rearing water. (2) The turbulence and shearing forces arising from direct aeration or spraying of tank water can be deleterious during the prefeeding and early feeding stages. (3) Although sea water can be more efficiently aerated than fresh water (Kils, 1977), the DO content of air-saturated sea water is about 20% less than that of air-saturated fresh water at the same temperature. (4) The toxicity of several substances, including ammonia, may be increased by decreases in DO (e.g., Lloyd, 1961). (5) Certain of the compensatory mechanisms available to fish with branchial respiration and haemoglobin, i.e., increasing opercular frequency and amplitude, and haemoconcentration, are obviously not possible during the phase of cutaneous respiration. Increased swimming activity or pectoral fanning might achieve the required ventilation, but at the cost of a higher metabolic rate.

The connection between low DO and loss of appetite reported by Stewart *et al.* (1967), among others, coupled with the above considerations, supports the proposition of Iwai & Hughes (1977) that the maintenance of adequate DO might be a very critical requirement for first-feeding success in marine fish larvae.

The literature on the effects of carbon dioxide on fish physiology and survival is not extensive; it has been reviewed by Doudoroff & Katz (1950), Fry (1957), and Jones (1964). In general, the reviewers conclude that fish are very tolerant of elevated concentrations of free carbon dioxide, particularly when they are allowed sufficient time to acclimate. Although the ability of fish to extract oxygen from surrounding water diminishes at abnormally high concentrations (the Root effect), the "ordinary environmental levels of carbon dioxide have little influence on the rate of oxygen consumption" in all but the "most sensitive species" (Fry, 1957). Fry stressed that considerable work needed to be done on the subject.

Aside from Kelley's (1946) experiment with herring (*Clupea harengus pallasi*) eggs, there appears to have been no attempt to determine the tolerance of marine fish eggs or larvae to elevated free carbon dioxide. The wide variation in carbon dioxide concentration during her experiment renders the results very difficult to interpret.

Materials and Methods

The general procedures follow those described by Brownell (1980). Dilution water used in all experiments (hereafter referred to as "system water") came from the closed-circulation system described in that publication. Specific methods pertaining to certain of the variables tested are treated separately below.

Tolerance Studies

LOW pH

Specific methods

Quantities of a concentrated (≈4 N) HCl stock solution were micro-pipetted into experimental feeding containers (see Brownell, 1980) holding system water, and the mixture was vigorously aerated for 1 h before measuring pH (NBS). Sixty minutes of aeration was found to be sufficient to reduce free carbon dioxide concentration to within 10% of equilibrium levels. If the resulting pH was not satisfactory, additional HCl or additional system water was added and aeration was resumed. The larvae were first transferred from the larva baskets into system water which had been acidified to about pH 3, aerated, and brought to neutrality by addition of sodium hydroxide. From there, they were pipetted into the test solutions. Food was re-suspended in a small quantity of the decarbonated water prior to addition. A second pH reading was taken at the end, after the incidence of feeding had been recorded and the larvae removed. The nominal pH was the arithmetic mean of the initial and final pH's recorded. Uncertainty as to the actual pH during exposure was greatest near the pH inflection point (≈pH 4.5). The computed 95% confidence limits were expanded by empirically derived values that took pH uncertainties into account. A normal distribution of tolerance over units of pH was assumed in the fitting of response curves.

Results and discussion

Three species were tested: a gadid, a soleid, and a sparid. Only the response curves for the gadid are presented here in graphical form (Fig. 1). For all three

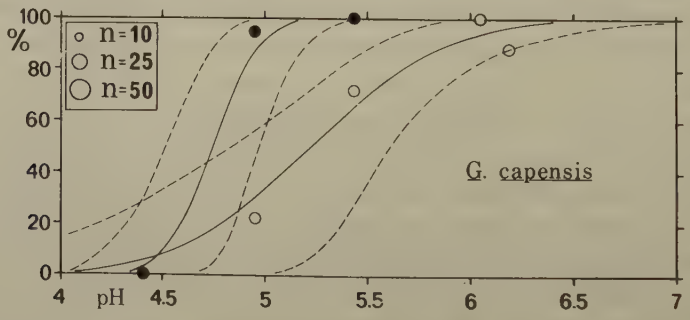

Fig. 1. Response of first-feeding *Gaidropsarus capensis* to low pH: open circles represent raw data (adjusted for natural responsiveness) on first-feeding incidence following 24-h exposure to various low pH's; solid circles represent data on percent survival during 24-h exposure; the areas of the circles are proportional to the number of larvae tested at corresponding pH's; the 95% confidence limits are represented by dashed lines.

TABLE I

ummary of tolerance limits: oxygen is expressed in mg · l^{-1}, carbon dioxide in mg · l^{-1} CO_2-C; the LC_{50}/EC_{50} ratios ıpplied for low and high pH are based on hydrogen and hydroxyl ion activities, respectively, and not on units of pH; 95% confidence limits are in parentheses.

Variable	Species	24-h first-feeding EC_{50}	24-h first-feeding EC_{10}	24-h LC_{50}	24-h EC_{10}	LC_{50}/EC_{50}
ow pH	*Gaidropsarus capensis* (Kaup)	5.22 (4.84–5.61)	5.91 (5.54–6.27)	4.74 (4.52–4.97)	4.99 (4.77–5.21)	3.0
	Heteromycteris capensis Kaup	5.25 (4.97–5.53)	5.90 (5.52–6.29)	4.48 (4.31–4.65)	4.51 (4.33–4.69)	5.9
	Diplodus sargus (L.)	5.20 (4.93–5.47)	5.69 (5.42–5.96)	5.06 (4.84–5.27)	5.17 (4.94–5.39)	1.4
ligh pH	*Gaidropsarus capensis*	8.67 (8.56–8.77)	8.39 (8.25–8.53)	9.24 (9.12–9.36)	8.99 (8.87–9.10)	3.7
	Heteromycteris capensis	8.78 (8.64–8.92)	8.50 (8.29–8.71)	9.21 (9.06–9.35)	8.92 (8.79–9.06)	2.7
	Diplodus sargus	8.82 (8.69–8.95)	8.52 (8.34–8.70)	9.04 (8.84–9.14)	8.89 (8.78–9.00)	1.7
O_2 static)	*Pterosmaris axillaris* (Boulenger)	4.77 (4.06–5.48)	5.66 (4.43–6.89)	3.49 (2.99–3.99)	3.98 (3.35–4.61)	0.73
	Pachymetopon blochi (Val.)	3.98 (3.24–4.71)	5.22 (4.12–6.31)	3.16 (2.67–3.66)	3.46 (2.89–4.02)	0.79
	Species 5 (Sparidae)			3.56 (2.92–4.20)	3.94 (3.15–4.73)	
	Trulla capensis Kaup.	4.30 (3.58–4.02)	5.41 (4.49–6.33)	<2.32		<0.54
	Gaidropsarus capensis	4.01 (3.26–4.76)	5.62 (4.56–6.67)	2.50 (1.78–3.23)	2.92 (2.25–3.60)	0.62
	Congiopodus spinifer (Smith)	4.04 (2.90–5.19)	5.30 (4.15–6.45)	3.63 (2.98–4.27)	4.21 (3.48–4.94)	0.90
O_2 low- hrough)	*Gaidropsarus capensis*	3.15 (2.43–3.86)	4.06 (3.15–4.97)	2.06 (1.58–2.55)	2.73 (2.08–3.38)	0.65
	Heteromycteris capensis	3.09 (2.26–3.93)	4.03 (2.29–5.08)	0.94 (0.55–1.32)	1.18 (0.80–1.57)	0.30
CO_2	*Heteromycteris capensis*	>7.7				

species (Table I), the 24-h first-feeding EC_{50}'s fell between pH 5.2 and 5.3; the 24-h LC_{50}'s, between pH 4.5 and 5.1. First-feeding began to be affected only as pH was reduced below about 6.0. The tolerance of these larvae came as a surprise. The data show that marine fish are about as tolerant of low pH as freshwater species, at least in the short term. Experiments on eggs and larvae of various freshwater species have yielded tolerance limits (variously defined) at pH's below 6.0 (e.g., Johansson & Kihlström, 1975; Milbrink & Johansson, 1975; Trojnar, 1977a, b). In the publications just cited, test solutions were allowed to equilibrate with atmospheric carbon dioxide prior to exposure. Almost all studies on freshwater fish eggs or larvae where free carbon dioxide concentration may have been large enough to affect the results yielded higher pH's as limiting values. No published information on the tolerance of marine fish eggs or larvae to low pH was encountered where a satisfactory distinction was made between toxicity due to hydrogen ion and that due to carbon dioxide.

From the results of the present study, it might be asserted that the maintenance of pH and carbonate alkalinity in closed and semi-closed fish culture systems at levels approximating those in the sea is unnecessary. This conclusion was reached by Hirayama (1970) who monitored pH and alkalinity (as well as ammonia and nitrate) in a small closed marine system in which juvenile sparids (*Acanthopagrus*) were kept. Alkalinity decreased linearly with time to a value of 0.2 meq $\cdot l^{-1}$ and pH below 6.0 with the fish showing no abnormal symptoms. Although a pH-related inhibition of nitrification has been reported, the nitrifying capacity of Hirayama's filter was still adequate to keep ammonia at a low level. The reward of operating a recirculating culture system at a lower pH would be the reduction in NH_3/NH_4^+ ratio. Before any such recommendation can be made, however, it will first be necessary to weigh the gain in ammonia ratio against possible long-term pH effects on fish larvae, bacteria, and ionic balance of the recirculating water.

HIGH pH

Specific methods

Varying amounts of a strong ($\approx$4 N) stock solution of NaOH in distilled water were added to system water in 350-ml test containers to yield an array of treatment concentrations. The solutions were then aerated for an hour, pH (NBS) was measured, and larvae were added. The pH of the water was again measured after the larvae had been removed. Change in pH during the 28-h experiments was caused primarily by addition of system water along with the fish and food (10 and 5 ml, respectively). The nominal pH was the mean of the initial and final pH's recorded. The 95% confidence limits of computed response curves were expanded by addition or subtraction of empirically determined values that took into consideration the instrument error in measuring pH and the variation in pH during tests. A model assuming a normal distribution of tolerance over units of pH was employed in the fitting of the response curves.

Results and discussion

Tolerance limits among the three species tested (a gadid, a soleid, and a sparid) were very similar: a 50% reduction in first-feeding incidence occurred at $\approx$ pH 8.7, 8.8, and 8.8 in the gadid, soleid, and sparid, respectively (Table I). A 10% reduction occurred at $\approx$pH 8.4, 8.5, 8.5, respectively. 24-h LC_{50}'s obtained for the three species fell between 9.0 and 9.2. Based on inspection of the three response curves (one of which is presented here, Fig. 2), a negligible-effect pH is not likely to exceed pH 8.4. This value is only marginally higher than the more extreme pH's recorded in the open sea (pH 8.3: Sverdrup *et al.*, 1942), and in light of the trend toward rearing marine fish larvae in green water, might pose a serious limit for the nurseryman.

Comparisons of these values with those of previous workers is difficult. Schach (1939) reported the limits of tolerance for herring (*Clupea harengus*) larvae as pH 8.45, and the optimal range as 8.2–8.3, but failed to explain the source of these values. Bishai's (1960) herring larvae died when the pH was raised from 8.1 to 8.5 by addition of $NaHCO_3$. The number of larvae tested and the final concentration of bicarbonate was not reported. Kelley (1946) found that Pacific herring eggs hatched a day sooner when they were incubated at pH 8.68 (range during exposure: 7.93–8.96), but that percent survival through hatching was not different from controls. A marked decrease in hatchability occurred in another experiment when pH rose to 9.12. No other data on the tolerance of the early stages of marine fish to elevated pH appear to be available.

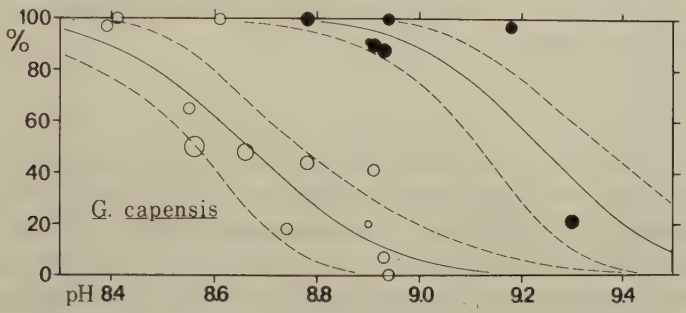

Fig. 2. Response of first-feeding *Gaidropsarus capensis* to high pH: other features as in Fig. 1.

A certain amount of acclimation to elevated pH has been demonstrated in juvenile rainbow trout by Jordan & Lloyd (1964). The improved growth rate of juvenile sole (*Solea solea*) over a 13-day period in tanks where the pH averaged ≈8.4 and rose eventually as high as 8.8 (due to phytoplankton production) (Alderson & Howell, 1973) suggest either that acclimation to elevated pH occurs among juvenile marine fish, or that they are simply more tolerant than larvae. It may be that the marine larvae in the present study, given a more gradual exposure increase, would have better tolerated high pH's. Further research on the response of fish larvae, both freshwater and marine, to elevated pH (particularly that associated with phytoplankton blooms) is needed.

DISSOLVED OXYGEN

Specific methods: static tests

System water, de-oxygenated to varying degrees by nitrogen stripping, was placed in test containers. Oxygen concentration was measured with a YSI-57 oxygen meter and probe. Larvae were introduced by pipette (along with 10 ml of system water) and the container was closed with a screened bung into which a small wad of synthetic wool had been pressed. After 24 h, the wool plug was removed, food

was added, and the plug was replaced in the bung. Oxygen was again measured immediately after the larvae had been rated for gut-fullness and removed.

Increases in the oxygen concentration during the course of the experiments came as a result of diffusion of atmospheric oxygen through the wool plug, by addition of oxygen with larvae and food, and during removal of larvae; decreases resulted from respiration by bacteria, food, and fish. A relationship of the oxygen concentrations measured at the beginning and end to the average concentration to which larvae were actually exposed was derived by fitting curves to measurements made during dummy runs. This permitted the calculation of an estimate of this average concentration for use as a nominal value in fitting response curves. Upper and lower 95% confidence limits were expanded by addition and subtraction, respectively, of empirically determined values to account for instrument error and variation in oxygen during exposures.

Specific methods: flow-through tests

The flow-through apparatus (Fig. 3) accommodates one control and four treatments. Water from the closed circulation system is de-oxygenated to varying degrees in a nitrogen stripping column, passed through the test containers holding the larvae, re-oxygenated, and returned to the system. Flow rate through each test container was maintained at 20 ± 2 ml $\cdot$ min^{-1}, which was sufficient to exchange 90% of the water in the containers every 40 ± 3 min. This gravity-feed system, similar to that described by Granmo & Kollberg (1972) was found to be very reliable. Variation in flow rate due to bubble formation in the tubing was not a problem as long as the head was >20 cm. For additional assurance, a 150 ml $\cdot$ min^{-1} diaphragm pump (Fig. 3) was used to dampen the effect of any variation in flow through one or more of the treatment channels.

At the end of the 24-h exposure, a count of survivors was made visually, without disconnecting the containers. A concentrated suspension of rotifers was then equally distributed among the five bubble traps. After 4 h exposure to food, one container at a time was disconnected, replaced by a container full of system water only, and then examined in the usual manner with the suspended microscope. In this way, the oxygen levels in the remaining containers were not affected by a decrease in the flow-rate of water through the column while the feeding incidence was being determined. Confidence limits of computed response curves were adjusted to account for instrument error and variation in oxygen concentration during the test. For both static and flow-through data, response rate was linearized by assuming a normal distribution of tolerance over un-transformed units of DO concentration.

Results and discussion

Results are presented for six species tested in static water and two species with the flow-through apparatus (Table I). Response curves for one species are pre-

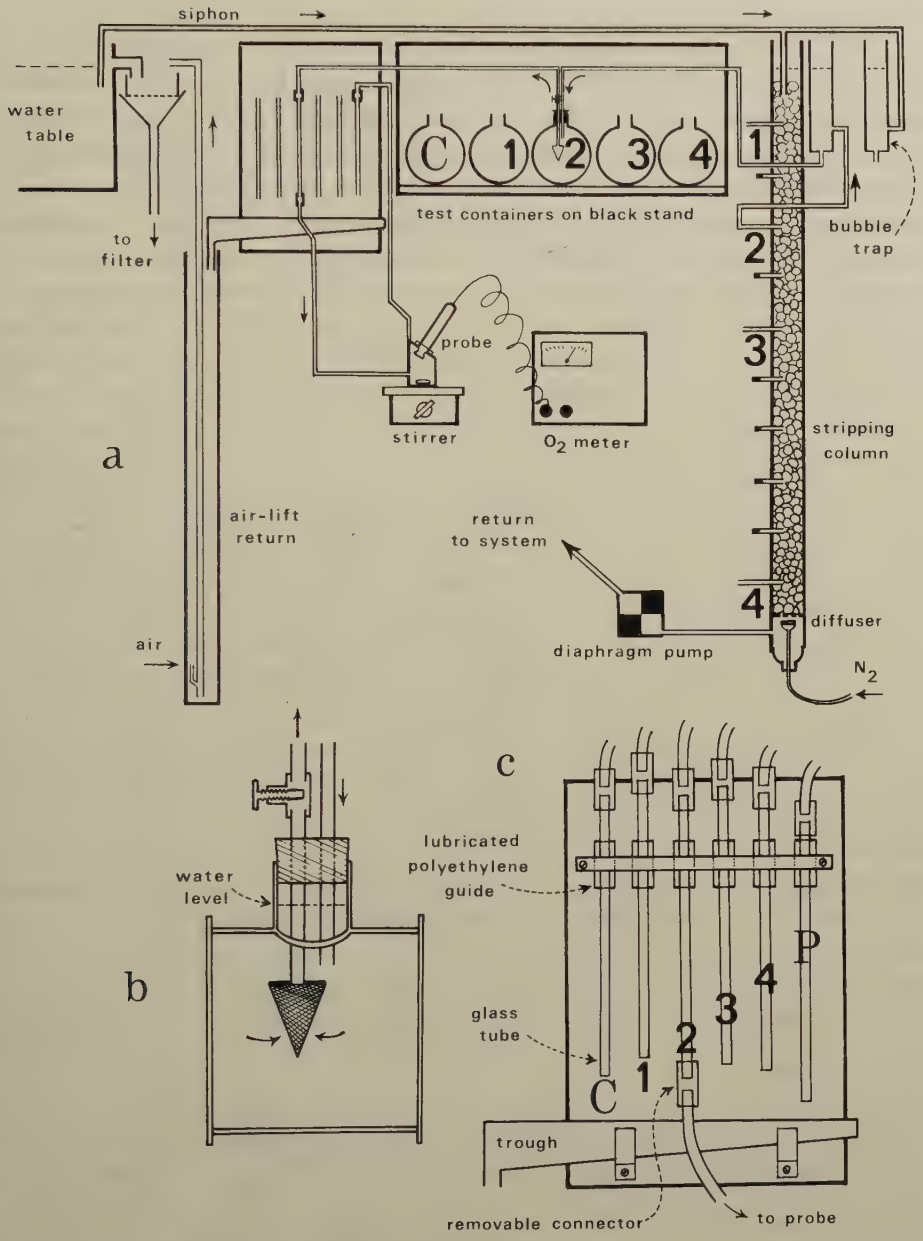

Fig. 3. The flow-through apparatus used for testing the tolerance of first-feeding larvae to low dissolved oxygen: a, general view, not to scale, only one channel (treatment No. 2) is shown, with probe circuit attached, two of the five bubble traps are shown; b, side view of test container with conical 40-μm mesh and valve on outlet; c, flow-control device, rate of dripping was regulated by raising or lowering the glass tubes.

sented (Figs. 4, 5). First-feeding incidence in all species was reduced by 50%, in a static test, when the DO concentration of the water mass was between ≈4.0 and 4.75 mg · l^{-1}. Caution must be exercised in predicting the response at more extreme percentiles. Although calculated EC_{10}'s (Table I) would suggest a somewhat higher value, the raw data show that the DO concentration at which first-feeding "begins" to be affected falls somewhere between 5.0 and 5.5 mg · l^{-1} for these same species. The discrepancy arises partly from the low weighting coefficients that are assigned to extreme response rates in maximum likelihood estimation, and partly from the somewhat horizontal distribution of data points in the area of median response (e.g., Fig. 4). Under conditions of temperature and salinity employed, these limiting values correspond to air-saturation percentages of 49–58% (4.0–4.75 mg · l^{-1}) and 62–68% (5.0–5.5 mg · l^{-1}) (Weiss, 1970). 24-h LC_{50}'s under static conditions were quite low in the case of the cynoglossid and gadid, but higher for the perciform species and the congiopodid (Table I).

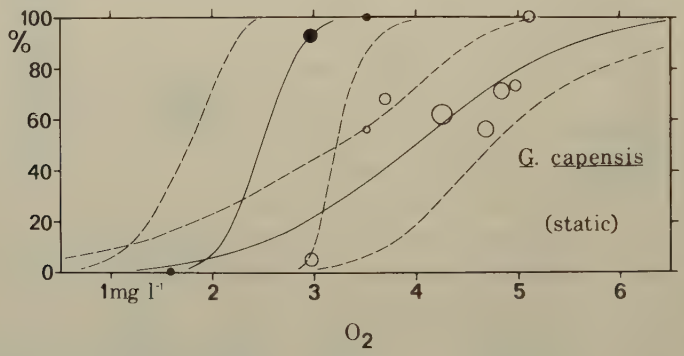

Fig. 4. Response of first-feeding *Gaidropsarus capensis* to low dissolved oxygen under static conditions: other features as in Fig. 1.

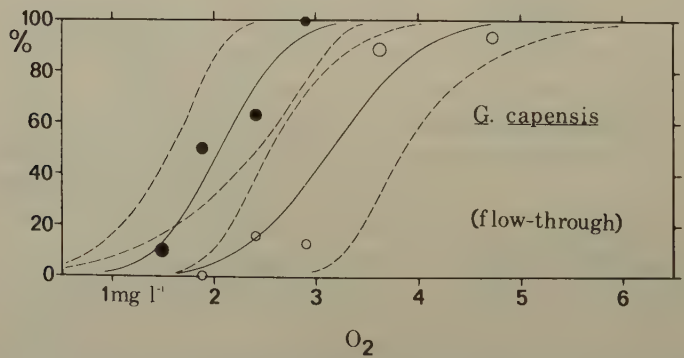

Fig. 5. Response of first-feeding *Gaidropsarus capensis* to low dissolved oxygen under flow-through conditions: other features as in Fig. 1.

Somewhat lower DO concentrations were found to be limiting when the flow-through apparatus was used (Table I, Fig. 5). All the first-feeding larvae tested in this study alternate between states of activity and rest. It is clear that in non-turbulent water, any decline in activity would enhance the oxygen-sink effect, whereas in turbulent water, a decline in activity might be negligible. De Silva & Tytler (1973) showed that herring and plaice larvae lowered their rate of oxygen uptake when the ambient concentration of DO was reduced. The decline in metabolic rate was apparently achieved by a decrease in activity. Since successful first-feeding requires considerable activity, there is a good theoretical basis for the results obtained.

CARBON DIOXIDE

Specific methods

Larvae of one species (*Heteromycteris capensis*) were exposed to a range of free CO_2 concentrations from 0.46 to 7.7 mg $\cdot l^{-1}$ CO_2-C. Elevated CO_2 concentrations were achieved by first increasing the alkalinity of system water by adding varying amounts of 0.4 M Na_2CO_3, then reducing the pH to 7.1–7.2 with 0.8 N HCl. It had already been established that, as long as CO_2 is in atmospheric equilibrium, first-feeding in *H. capensis* is not impaired by a 24-h exposure to pH's as low as 6.5, nor by bicarbonate concentrations of that of the most extreme treatment group tested, i.e., 8.9 mmol $\cdot l^{-1}$.

The tests were static. The test containers were fitted with screened bungs packed with a wad of synthetic wool, turned face-down, and left for 24 h. As usual, food was added and larvae were given 4 h to feed. After rating and removing larvae, the final pH was measured and the total alkalinity was determined by titration with 0.010 N HCl. The nominal concentration of free CO_2 was taken as the amount calculated to be present at the end of the experiment. The relationships and constants required for the evaluation of the carbonate system in sea water were taken from Skirrow (1965).

Results and discussion

There were no noteworthy differences in first-feeding incidence between the control and any of the treatments (Table II). The highest level of CO_2 tested was 7.70 mg $\cdot l^{-1}$ CO_2-C, which corresponds to 28 mg $\cdot l^{-1}$ CO_2, or a P_{CO_2} of 1.69 kPa under the conditions specified (Murray & Riley, 1971).

The only study encountered on the tolerance of marine fish eggs of larvae to free CO_2 was that of Kelley (1946), who incubated Pacific herring eggs in the presence of elevated CO_2 (achieved by bubbling CO_2 gas into incoming water). She reported a serious retardation in embryonic development and failure to hatch. Wide variation in the exposure concentration (2.1–18.5 mg $\cdot l^{-1}$) and pH (5.12–7.88) detract from

TABLE II

Results of an experiment in which first-feeding *Heteromycteris capensis* were exposed to free CO_2 concentrations of 0.46 (control) to 7.70 mg $\cdot l^{-1}$ CO_2-C.

	pH at end	Total alkalinity (meq $\cdot l^{-1}$)	HCO_3-C (mg $\cdot l^{-1}$)	CO_3-C (mg $\cdot l^{-1}$)	CO_2-C (mg $\cdot l^{-1}$)	Number of larvae with: Gut full	Gut ½-full	Gut nearly empty	Gut empty	Σn	% "fe
Control	7.83	2.45	26.89	1.02	0.46	18	2	0	1	21	95
Treatment 1	7.09	0.75	8.79	0.06	0.82	12	5	1	1	19	89
Treatment 2	7.16	3.60	42.41	0.34	3.36	15	4	3	0	22	86
Treatment 3	7.17	6.00	70.72	0.58	5.48	16	4	0	2	22	91
Treatment 4	7.20	9.05	106.59	0.94	7.70	14	4	1	1	20	90

the usefulness of the data. Putnam (1967, unpubl., reviewed by Doudoroff & Shumway, 1970) found that an exposure of rainbow trout eggs during the entire incubation period to 7.7 mg $\cdot l^{-1}$ CO_2-C had little or no effect on the mass of the newly-hatched larvae (minus yolk) as long as dissolved oxygen was adequate.

The Cape sole is admittedly one of the more rugged of the 10 species of larvae used in these studies, and one cannot automatically rule out the possibility that first-feeding in one of the other species would have been affected at the highest concentrations tested. Still, 7.7 mg $\cdot l^{-1}$ is well above the levels of free CO_2 likely to be present in any fish tank. Because excess CO_2 is lost to the atmosphere through the same procedures by which DO is introduced, the chances that free CO_2 could become the primary limiting factor in an adequately oxygenated rearing tank are extremely remote.

General Discussion

Of the four variables treated here (low and high pH, dissolved oxygen, and carbon dioxide) and the three treated earlier (ammonia, nitrite, and nitrate) (Brownell, 1980), only high pH, low dissolved oxygen, and un-ionized ammonia significantly inhibit first-feeding at levels likely to be encountered in a rearing tank for larval marine fish. Although attention is directed to the potential danger of inadequate control of the last three variables, it is clear that other reasons must be found to account for failure of some larvae to feed in captivity. In these studies, $\approx 20\%$ of all tolerance experiments were rejected because the feeding incidence in control groups was below an arbitrary 50%. Mean control feeding incidence in the remainder was 74.8%. Certain species (*Heteromycteris capensis*, *Gaidropsarus capensis*, *Pachymetopon blochi*, and *Congiopodus spinifer*) only rarely yielded control feeding incidences below 50%; others (*Trulla capensis* and *Synaptura kleini*) were extremely variable, often falling below 50% but occasionally approaching 100%. In the bioassay experiments conducted by Lasker (1975), control feeding incidence (defined as the

presence of more than eight particles in the gut at the end of an 8-h exposure to food) ranged from 27 to 32%. About the same percentage had 1–8 particles of food in the gut. The remainder had consumed no food at all. A consumption rate of at least one particle/h had been established in the laboratory as the minimum for survival.

Whether to attribute the often high degree of first-feeding incompetence to factors related to the captive situation, or to blame fundamental disfunction, is a difficult decision at this time. There is tremendous scope for future work on both environmental and genetic factors that influence the ability of a marine fish larva to ingest its first particle of food.

Acknowledgements

I thank the Fisheries Development Corporation of South Africa for their sponsorship, and in particular H. Champion and C. G. du Plessis of that organization for their interest and support of this project. I thank A. Brown for his kind assistance during the publication of this work.

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